17.

The Phylogeny of the Characin Fishes.

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(Text-figures 1-37).

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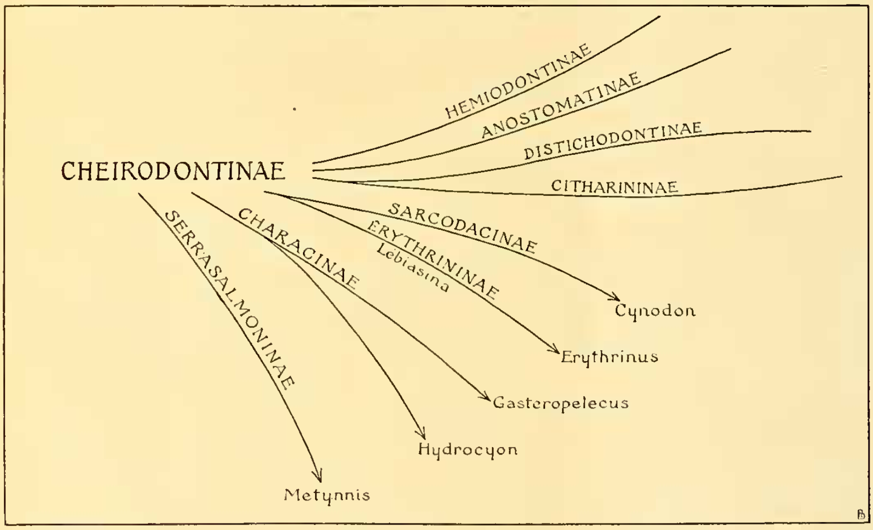
INTRODUCTION.

In the systematic history of the family Characinidae, among the greatest contributors were Müller and Troschel (1844, +), Sagemehl (1884, +), Boulenger (1887, +), Eigenmann (1899, +), Rowntree (1903, 1906), and Regan (1911, +). In spite of all of these labors the broad evolutionary trends were so easily obscured by the details that it was only in 1917, with the publication by Eigenmann of the first part of his monograph on "The American Characidae," that the first attempt to outline the phylogenetic relationships of all of the South American subfamilies was made (Text-fig. 5). Unfortunately this outline from which we have made a phylogenetic diagram was never completely developed, for Dr. Eigenmann died before the completion of his memoir on the Tetragonopterinae and allied subfamilies.

Rowntree (1903) examined the visceral anatomy of the characins and made several contributions of phylogenetic interest, including evidence against the idea of an amioid ancestry of the Erythrininae which had been suggested by Sagemehl. Much of the data concerning the visceral anatomy merely shows the differences in adaptation to an herbivorous diet on the one hand and a carnivorous diet on the other. Thus the differences and similarities noted in the stomach and intestine have little phylogenetic significance of subfamily rank, inasmuch as the herbivorous condition has apparently been developed independently several times within the family.

In 1911 Regan revised the classification of the Characinidae and in so doing synthesized the groups of previous authors to a more workable system. However, in many respects the classification of Boulenger in the Cambridge Natural History is still useful.

Cockerell (1912, 1913) studied the scales of both the African and South American characins. His studies were very detailed and in some cases his results are confusing when compared with other data, but on the whole they served to clarify the phylogenetic relationships within certain groups.



Text-figure 1.
The phylogenetic relationships of the subfamilies of the Characidae.

The fossil records of this group are very meagre. From the Tertiary of Brazil and Peru three more or less doubtful genera are known: *Lignobrycon*[1] Eigenmann and Myers 1929, *Eobrycon*[2] Jordan 1907, *Characilepis* Cockerell 1920. These are apparently related to the Characinae. The teeth known as *Onchosaurus* Gervais 1852, which are found in the Upper Cretaceous of North America, Europe and Egypt, have been shown by Eastman (1917) to resemble the teeth of *Hydrocyon* and *Hoplias*. However, neither in general body form nor in tooth structure are any of these genera primitive and we must, therefore, with Eigenmann, fall back upon an analysis of the generalized conditions among living characins as the principal basis for a tentative reconstruction of phylogenetic history.

As a basis for our chart (Text-fig. 1) of the phylogenetic relationships of the family Characinidae we have used first the monumental work, "The American Characidae," by C. H. Eigenmann, as well as many lesser papers by the same author. Nor have we neglected the important systematic and distributional studies of Regan, Boulenger and others. Our own material includes a series of skeletal and preserved specimens representing the vari-

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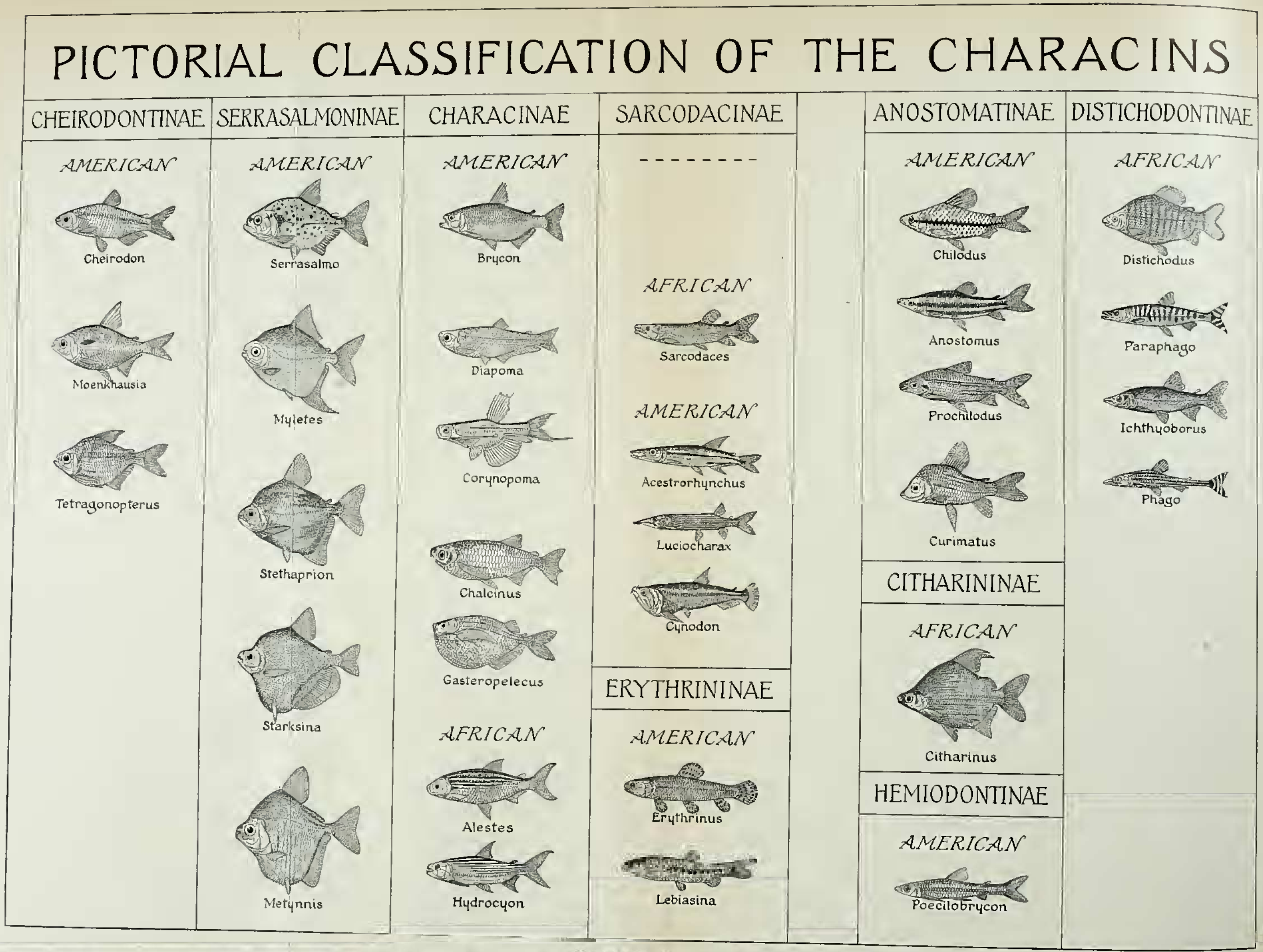
[1] Based on *Tetragonopterus ligniticus* Woodward, Catalogue of Fossil Fishes in the British Museum (Natural History), 1901, pt. 4, p. 298, pl. 17, figs. 2, 3.

[2] Based on *Tetragonopterus avus* Woodward, ibid., p. 298, pl. 17, fig. 1.

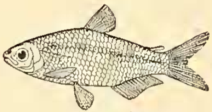


Text-figure 2.
A pictorial classification of the characin fishes.

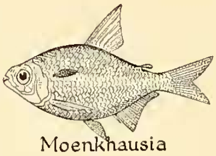
PICTORIAL ACINS

CHEIRODONTINAE

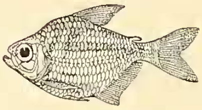
AMERICAN



Cheirodon



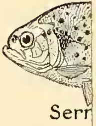
Moenkhausia



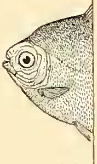
Tetragonopterus

SERRAS

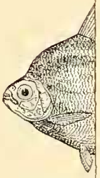
AME



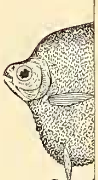
Serr



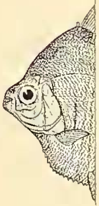
My



Steth



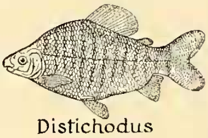
Stark



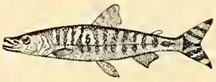
Met

DISTICHODONTINAE

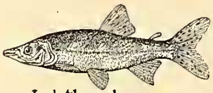
AFRICAN



Distichodus



Paraphago



Ichthyoborus

Phago

ous subfamilies; especially those brought back by Messrs. Lang and Chapin of the American Museum Congo Expedition of 1909-1915, and the Brazilian collections made by B. A. Krukoff in 1934 and 1935.

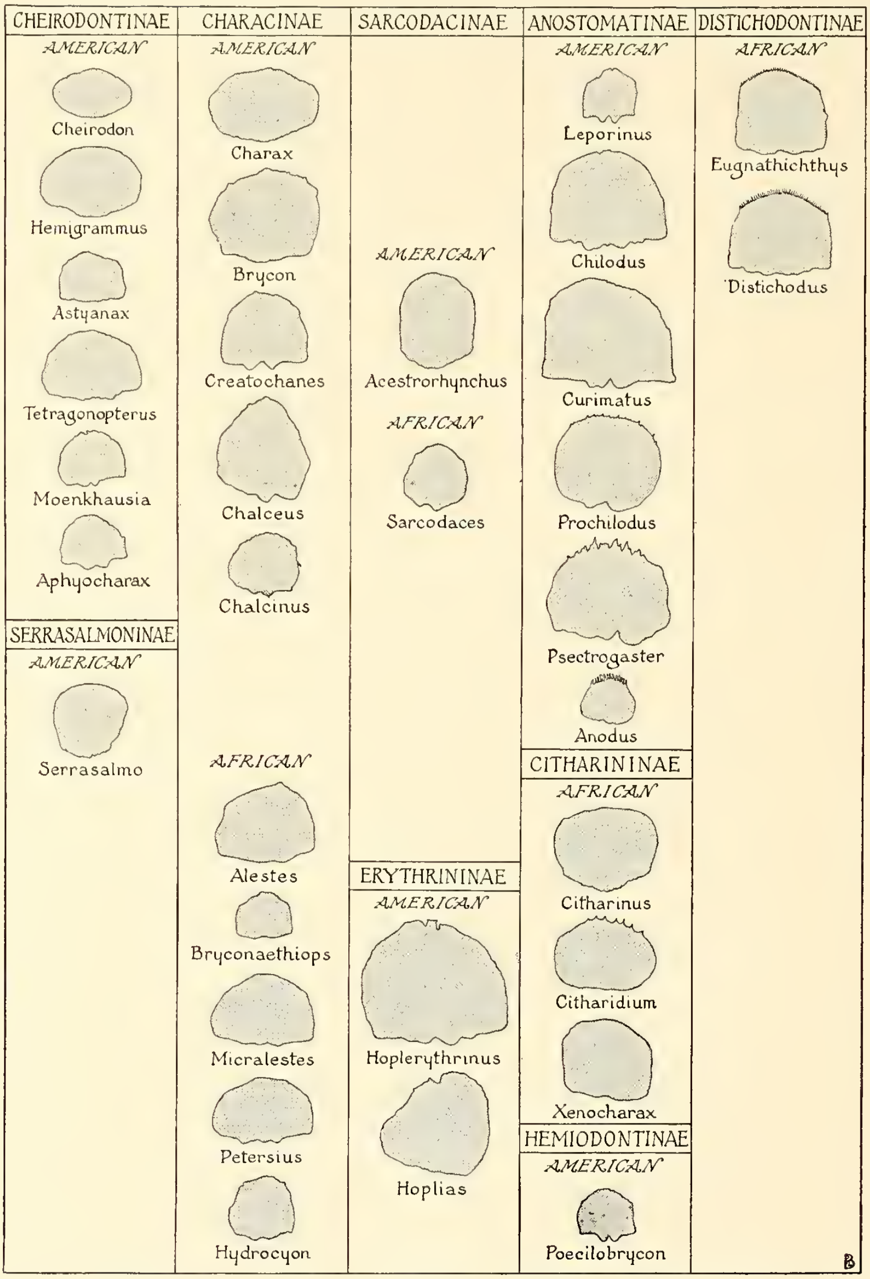
As an aid to the construction of a tentative phylogenetic chart we have arranged a "Pictorial Classification of the Characins" (Text-fig. 2). This is based on a phylogenetic interpretation of the characters used in defining families, subfamilies, etc., by various authors. In view of the remarkable uniformity in basic morphology of all characins and of the existence of more or less annectant genera between the so-called families of earlier authors we have treated the entire series as a single family, Characinidae, coordinate in rank with the Gymnotidae, the latter being an extremely specialized and presumably early side branch.

To supplement the chart showing the inferred phylogenetic relationships of the general body forms we have added several other charts laid out on the same plan. First of these is a series of scales as figured by Cockerell (1912, 1913). Although Cockerell figured the circuli and radii of the scales, we have contented ourselves with the outlines (Text-fig. 3) which, by themselves, seem to present the several broad divergent trends within the family.

A series of diagrams of characin livers has been compiled from Rowntree's data. These drawings (Text-fig. 4) are quite schematic and are merely diagrams from verbal descriptions, but they afford an interesting contrast to the more or less stable characters relied on in the above charts. Whether the viscera, always in a more or less plastic state, have any really helpful significance in these studies is open to question except in certain cases, but it is noteworthy that in several places interrelationships are evident.

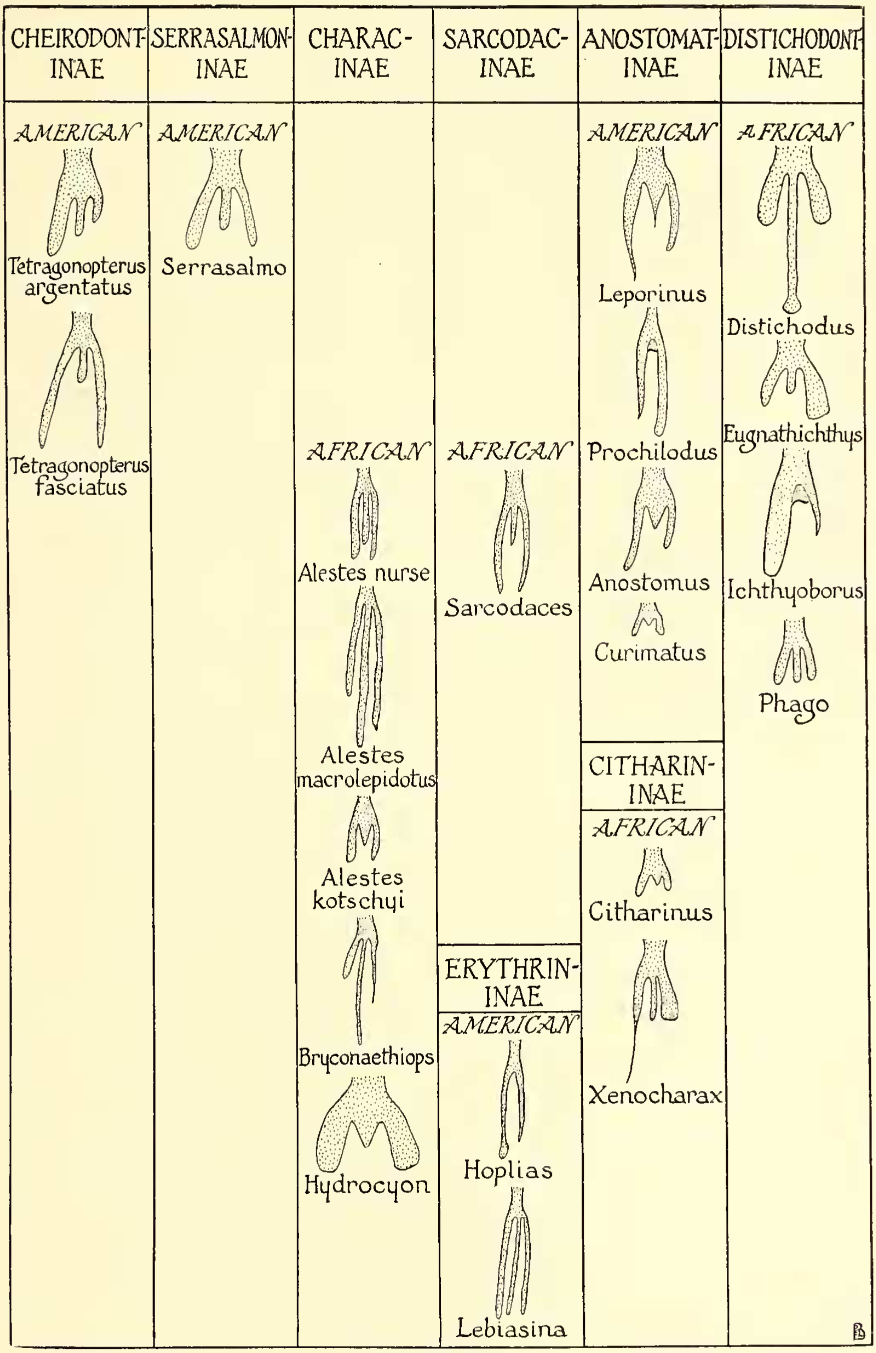
For convenience we insert at this point a summary of the subfamilies of the characins, as used in the present paper.

1. Cheirodontinae (Cheirodontinae and Tetragonopterinae of Eigenmann). Primitive, generalized characins; both maxilla and premaxilla bearing teeth; marginal teeth varying from pluricuspid to conical; mouth moderate to small. American: *Grundulus, Mixobrycon, Moenkhausia* (Text-figs. 2, 8), *Tetragonopterus* (Text-figs. 2, 7, 8), *Cheirodon* (Text-figs. 2, 6, 8), etc.
2. Serrasalmoninae (Stethaprioninae, Serrasalminae and Mylinae of Eigenmann). Extremely deep bodied; short, heavy jawed offshoots of *Tetragonopterus.* Nicely graded series of constantly increasing ratios of depth to length. Teeth grade from carnassial to molariform. American: *Stethaprion* (Text-fig. 2), *Mylesinus, Serrasalmo* (Text-fig. 2), *Mylosoma* (Text-figs. 7B, 8), *Metynnis* (Text-fig. 2), etc.
3. Characinae (Characinae (in part), Hydrocyoninae and Gasteropelecidae of Regan). The large central group of African and South American forms arising from the Cheirodontinae. Varying in body-form, but central type as in *Brycon;* hypocoracoids usually forming prominent vertical laminae, but grading into forms with short median laminae and divergent coracoid fossae (*Cynopotamus*); lateral line decurved; no teeth on palatines. American: *Charax, Brycon* (Text-figs. 2, 9, 11, 12, 14, 16, 30), *Iguanodectes, Diapoma* (Text-fig. 2), *Corynopoma* (Text-fig. 2), *Chalcinus* (Text-figs. 2, 13, 14), *Gasteropelecus* (Text-figs. 2, 13, 14). African: *Alestes* (Text-figs. 2, 10, 15), *Hydrocyon* (Text-figs. 2, 11, 12, 17, 18, 19, 20, 21, 29).
4. Sarcodacinae (Sarcodacinae, Acestrorhamphinae, Cynodontinae and Xiphostomatidae of Regan). Predatory "pikes" derived from the Characinae. Jaws more or less elongate with caniniform teeth; a large prefrontal plus supraorbital bone; supraoccipital small, not elevated above flattened skull top; no interfrontal fontanelle. Ameri-



Text-figure 3.

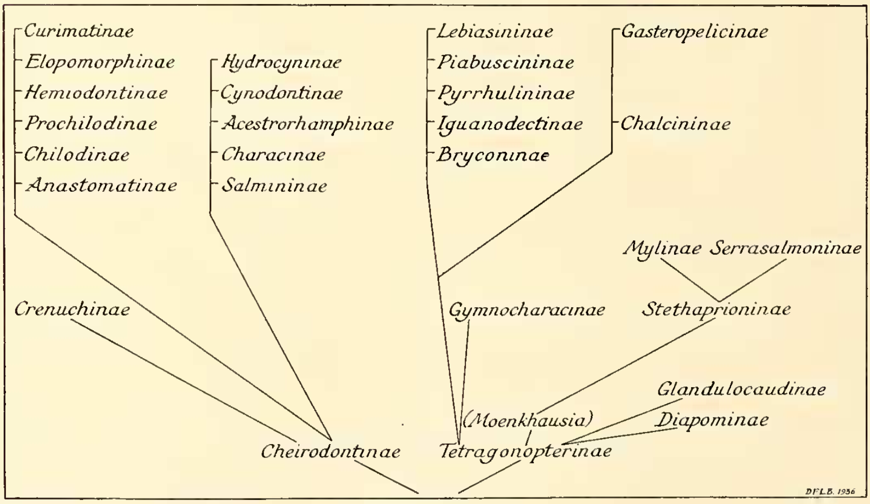
Chief variants in the form of characin scales. Based on data from Cockerell (1912, 1913).



Text-figure 4.
Chief variants in the form of the liver. Based on Rowntree's (1903) data.

can: *Luciocharax* (Text-figs. 2, 23, 24), *Acestrorhynchus* (Text-fig. 2). African: *Sarcodaces* (Text-figs. 2, 23, 24).

5. Erythrininae (Erythrininae and Lebiasininae of Regan). *Amia*-like relatives of *Sarcodaces* with more or less broad, rounded heads. Opposite hypocoracoid fossae diverging sharply, median laminae short (*Lebiasina*) to absent; lateral line straight (lacking in *Lebiasina*). Teeth on palatines. American: *Erythrinus* (Text-figs. 2, 25, 26), *Hoplias* (Text-fig. 24), *Lebiasina* (Text-fig. 2).
6. Hemiodontinae (Hemiodontidae of Regan). Small fusiform to slender offshoots of the Characinae with short anal fin, adipose typically reduced or absent; very small to small subterminal to terminal mouth; teeth uniserial, minute; "pterygoid movably articulated with quadrate, narrowed posteriorly ending in a small condyle" (Regan). American: *Hemiodus, Poecilobrycon* (Text-fig. 2), *Nannostomus, Parodon.*
7. Anostomatinae (Anostomidae of Regan). Slender to deep-bodied herbivorous American characins. In scale and jaw characters paralleling some of the Citharininae and Hemiodontinae. "Pterygoid rather broad posteriorly, overlapping the quadrate" (Regan). *Anostomus* (Text-fig. 2), *Prochilodus* (Text-fig. 2), *Chilodus* (Text-fig. 2). *Curimatus* (Text-figs. 2, 28), *Leporinus* (Text-figs. 28, 29, 30, 31, 32).
8. Citharininae (Citharininae, Hemistichodontinae and Xenocharacinae of Regan). An African group grading in scale characters from cycloid to ctenoid. Parallel in many characters to South American Anostomatinae. *Citharinus* (Text-fig. 2), *Xenocharax.*
9. Distichodontinae (Distichodontinae and Ichthyoborinae of Regan). This African group seems to be related to the Citharininae, but is sharply separated in that the dentaries are movably articulated with the articulars. *Distichodus* (Text-figs. 2, 33), *Phago* (Text-figs. 2, 35), *Ichthyoborus* (Text-fig. 2), *Mesoborus* (Text-fig. 34), *Paraphago* (Text-fig. 2).



Text-figure 5.

The phylogeny of the South American characins, according to Eigenmann (1917, pp. 38, 39).

PHYLOGENETIC REVIEW OF PRINCIPAL GROUPS.

CHEIRODONTINAE.

Several authors, including one of us (Gregory, 1933), have considered the Erythrininae to be the most primitive existing subfamily of the Characinidae, but further study indicates that this subfamily is relatively high in the phylogenetic series. After close study of Eigenmann (1916), we are indeed forced to the conclusion that the Erythrininae are less primitive than the Cheirodontinae.

Text-figure 6 represents the skeleton of *Cheirodon.* It closely resembles the generalized cheirodont which Eigenmann has pictured for us in words. It is a relatively deep-bodied type, with a long anal fin having its origin under the last dorsal ray and reaching almost to the origin of the caudal. The caudal is deeply forked. The mouth is terminal and relatively small. The teeth of the generalized type are in a single series, rather few in number and with lateral notches, occurring along the edge of the premaxilla, at the upper angle of the maxillary, and along the front and sides of the lower jaw.

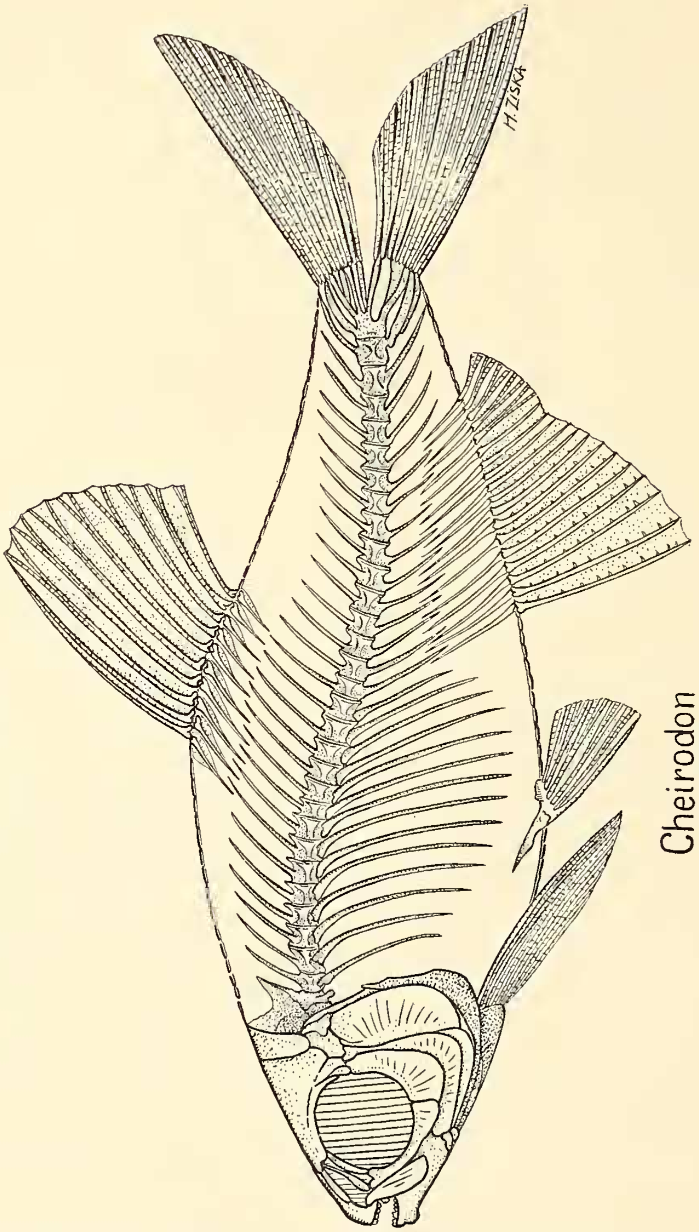
The Cheirodontinae, or some of them, also retain several other outstanding generalized characters from which those of almost any of the remaining subfamilies may have sprung. One of these is the extremely undifferentiated cycloid scales, almost elliptical in shape, from which the others have evidently developed. Another is the greatly variable tooth form, which, as noted by Eigenmann, ranges from the simple conical type of *Grundulus,* through the bicuspid teeth of *Macropsobrycon,* the tricuspids of *Aphyocharax, Megalamphodus, Parecbasis* to the octacuspids of *Cheirodon.* Thus, as far as teeth are concerned, this group is well prepared to account for all of the bizarre tooth-types encountered in the family, such as the caniniform teeth of *Hydrocyon,* the molariform teeth of the Mylinae, the incisor-like teeth of *Leporinus* and many others.

Eigenmann's generalized cheirodont exhibits the well developed chain of suborbital bones which are constantly cropping out in various genera of the Characinidae and which apparently first led Sagemehl to the belief that *Erythrinus* had amioid affinities (since wholly disproved by several authors). An adipose fin is present in the generalized type of the Cheirodontinae as well as in most other Characinidae. However, the cheirodont genera *Grundulus* and *Spintherobolus* lack one, this indicating that the possession of an adipose is in an unstable condition in even the more primitive characins. Some of the Cheirodontinae also have the median fronto-parietal fontanelle which is so frequent in other subfamilies.

Arising from the Cheirodontinae (*sensu strictu*), then, are the several diverging subfamilies. The Tetragonopterinae of Eigenmann are very near to the primitive stock of the characins and may have been derived from the Cheirodontinae or from a common stem. In either event Eigenmann points out the significant similarity of the heavy teeth and cheek armor in *Mixobrycon* (Cheirodontinae) and that of *Hyphessobrycon* (Tetragonopterinae). A glance at *Moenkhausia* (Text-fig. 2), a tetragonopterine, will show the general similarity of its body form to that of *Cheirodon pulcher. Tetragonopterus* proper (Text-fig. 2) is a greatly deepened form which through some species such as *T. argenteus* has given rise ultimately to the extremely deep-bodied and strangely modified Serrasalmoninae.

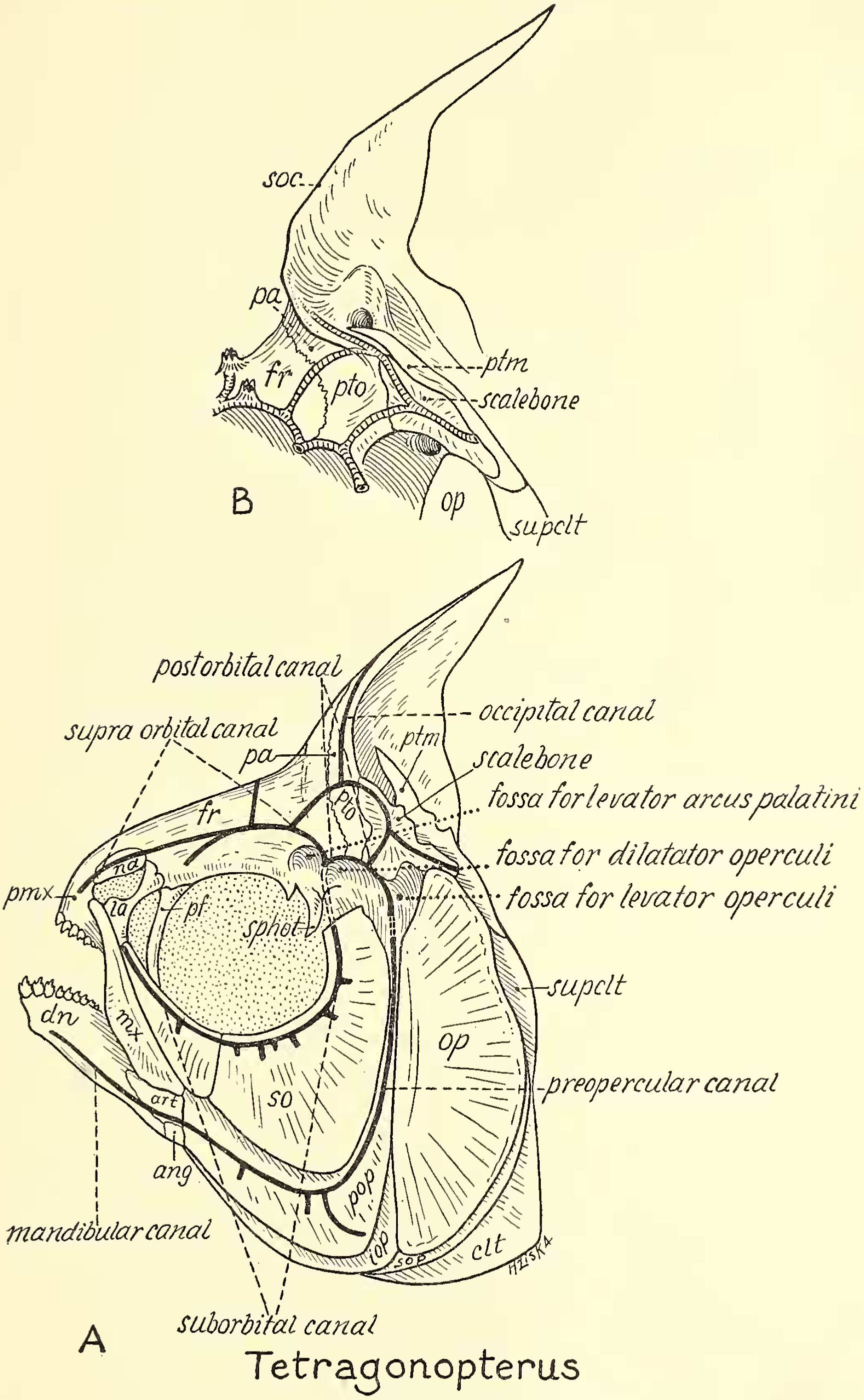
SERRASALMONINAE.

We have seen above that *Tetragonopterus argenteus,* which we refer to the Cheirodontinae, approaches very closely to the body form of the Stethaprioninae and differs from the latter chiefly in the lack of a "pre-dorsal spine" insofar as external gross characters are concerned. Both Cockerell



Text-figure 6.
Skeleton of *Cheirodon* (× 4).

(1913) and Eigenmann and Myers (1929) noted the relationship between *Stethaprion* and another cheirodont, *Moenkhausia*, but Eigenmann (1907) states, "the members of the Stethaprioninae mark the direct road from the genus *Tetragonopterus* in its *narrowest* sense to the Mylinae and Serrasalmoninae. In the deep *T. argenteus* the post-ventral region is trenchant, the pre-ventral region flat. In *Stichonodon* both pre-ventral and post-ventral regions are trenchant. In *Stethaprion, Brachychalcinus,* and *Fowlerina* the post-ventral region is incipiently serrate and there is a pre-dorsal spine.



Text-figure 7.

A, skull of *Tetragonopterus*, showing lateral line canals and principal muscle fossae. B, *Mylosoma*, detail of occipital region, showing canals.

In *Mylesinus* of the Mylinae the abdomen is serrate behind the ventrals and in the rest of the Mylinae and Serrasalmoninae the ventral edge is serrate both in front and behind the ventrals." This series is supported again by Eigenmann and Myers in 1929. On the entire chart of body forms (Text-fig. 2) there is no series so convincing as this one, especially in the constantly increasing ratio of depth to length until finally, in *Metynnis*, the depth almost equals the length. There is a transition from the sharp, shearing, carnassial-like teeth of *Serrasalmo* to the more blunt, molariform teeth of *Myletes*, while the jaws in both remain short and blocky. In liver form (Text-fig. 4) *Serrasalmo* appears to be very generalized.

The skulls of the Cheirodontinae and the Serrasalmoninae are often quite small and paper thin so that in order to facilitate the identification of the bones a detailed study of the sensory canals was made. Text-figure 7, an outline picture of the skull of the typical genus, *Tetragonopterus*, shows the position and names of the canals and the diagnostic muscle fossae.

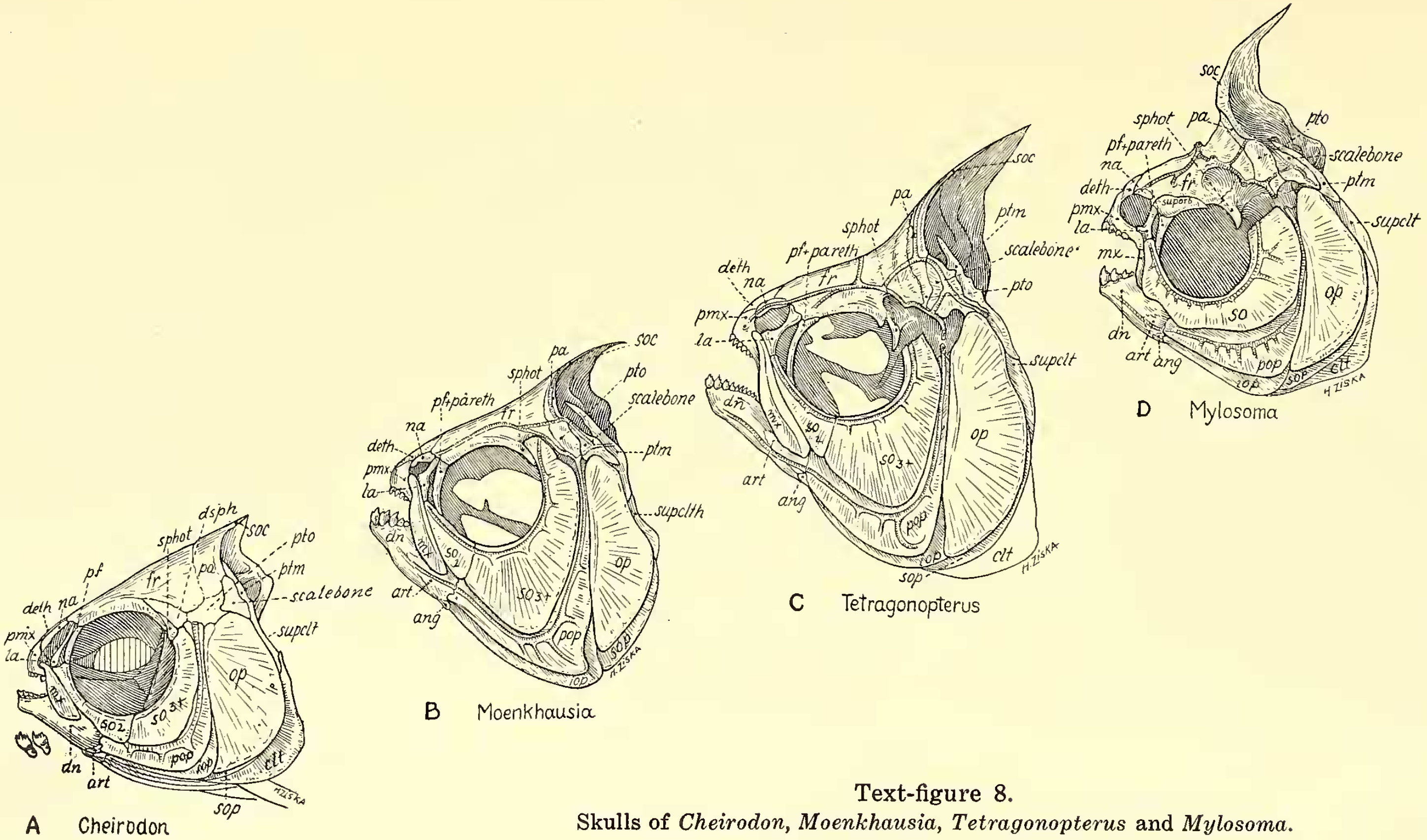
The lateral line passes from the body into the posttemporal bone and from there it continues into the "scalebone." In the scalebone it forks into two branches, one leading toward the postorbital canal, the other, the occipital canal, passing dorsally through the parietal bone. Just above the scalebone the occipital canal is met by a branch from the supraorbital canal. At the most ventral point of the surface of the pterotic the preopercular canal arises. This preopercular canal runs directly into the mandible. Starting at the origin of the preopercular canal and bordering the fossa of the dilatator operculi is the postorbital canal which continues forward to the junction of the suborbital canal with the main trunk. The suborbital canal joins the main canal at the "peninsula" which marks the separation of the fossa for the levator arcus palatini from that of the dilatator operculi. From this junction forward the sensory canal is known as the supraorbital canal and gives off several branches as it passes through the frontal bone. This canal passes through the nasal bone and, in *Tetragonopterus* at least, seems to continue into the premaxilla.

The nicely graded series of body forms which has been noted in the cheirodont-serrasalmonine branch is reflected in the skull structures. *Cheirodon* (Text-fig. 8A) has the skull of a more or less fusiform habitus. The dorsal curvature of the skull is slight and convex and there are sizable parietals, which might imply a lack of the forward curling of the occiput that is seen as we proceed up the scale. The dermosphenotic is present in this primitive form. The jaws are relatively compact and strong and are not elongate.

Moenkhausia (Text-fig. 8B) reflects the slightly deeper body and the supraoccipital crest is a bit more steep than in *Cheirodon*. Indeed the entire skull shows a dorso-ventral emphasis. The dermosphenotic disappears in *Moenkhausia* and is lost in those latter specimens of this series which we have examined. The parietal and pterotics have been reduced.

The skull of *Tetragonopterus* (Text-fig. 8C) resembles very closely that of *Moenkhausia*. As might be inferred from the progressively increasing body-depth, the supraoccipital bone is so upturned that the frontal is quite concave in side view. The suture between the frontals and the parietals and pterotics is in the form of two acute angled, overlapping bevels. Thus the surface extent of the parietals is a great deal less than the cranial. This suggests a mechanical shoving forward of the temporal region. The postorbital portion of the circumorbital chain has been dissected away so as to show the various muscle fossae as well as the postorbital process of the sphenotic bone.

As a representative of the Serrasalmoninae, *Mylosoma* (Text-fig. 8D) serves admirably. Here is the ultimate in the deep-bodied forms in some of which the depth almost equals the length. It is no wonder, therefore, that the fronto-parieto-supraoccipital contour in side view is so concavo-



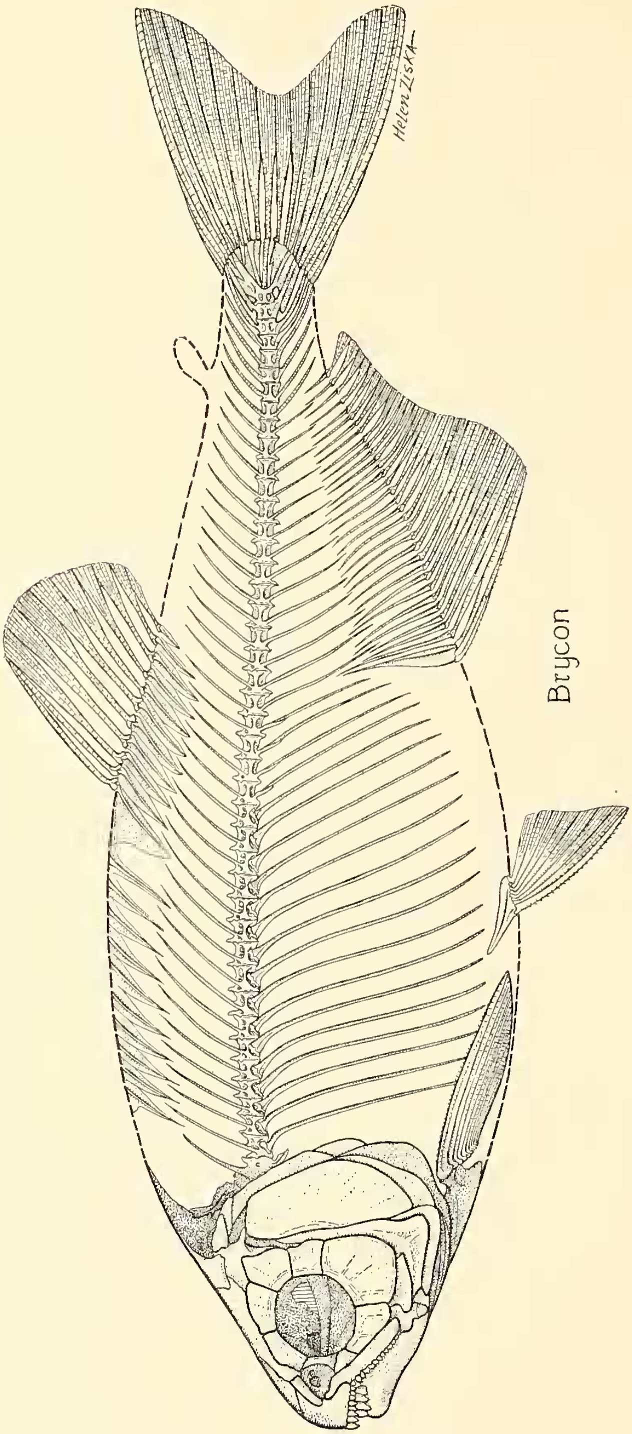
A Cheirodon

B Moenkhausia

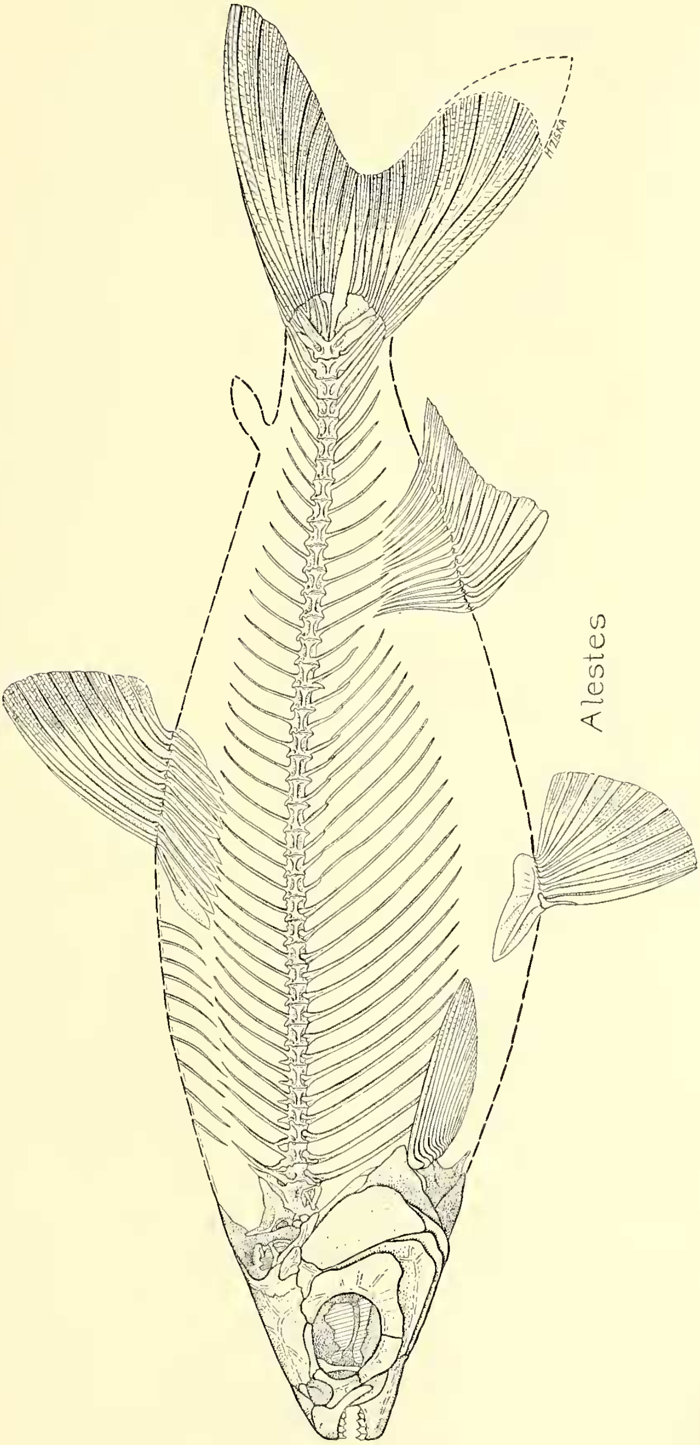
C Tetragonopterus

D Mylosoma

Text-figure 8.
Skulls of *Cheirodon*, *Moenkhausia*, *Tetragonopterus* and *Mylosoma*.



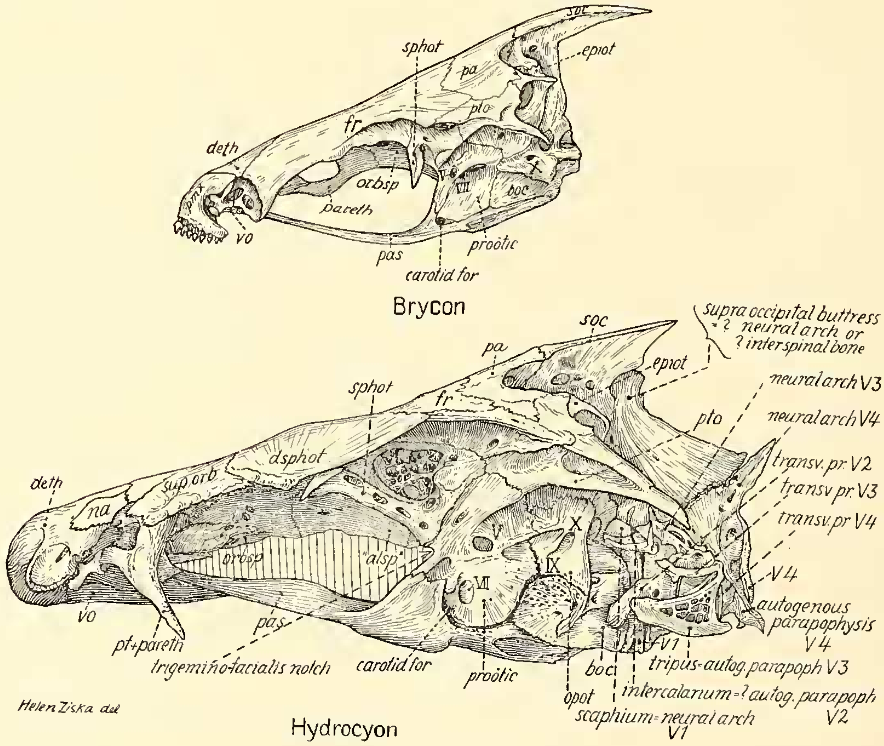
Text-figure 9.
Skeleton of *Brycon*.



Text-figure 10.
Skeleton of *Alestes*.

convex as to form a feeble S. In *Tetragonopterus* a perpendicular line passing through the posterior tip of the supraoccipital would also pass close to the rear margin of the operculum, while in *Mylosoma* such a line would pass through the center of the postorbital portion of the circumorbital chain. For the first time in this series a new bone appears, the supraorbital. The sensory canal system retains the basic plan of Text-fig. 7A, but in response to the necessity of the openings passing through the thick layer of fatty tissue (which cushions the concave part of the skull) there have been developed several bony "craters" which carry the canals to the surface. The word, crater, is really descriptive of them for they look much like a volcanic crater—an eruption of the bone. As another innovation the occipital canal passes behind the crest, which is usually placed at the posterior edge of the parietal. However, in *Mylosoma* this crest has moved forward on the parietal, while the canal presumably maintains its primitive position (see inset, Text-fig. 7B).

The most salient feature of this phylogenetic branch is the constant anterior movement of the occipital region while the rest of the skull remains stationary. The loss of the dermosphenotic and the appearance of the supraorbital are observed. The fontanelles are left intact throughout the group.



Brycon

Hydrocyon

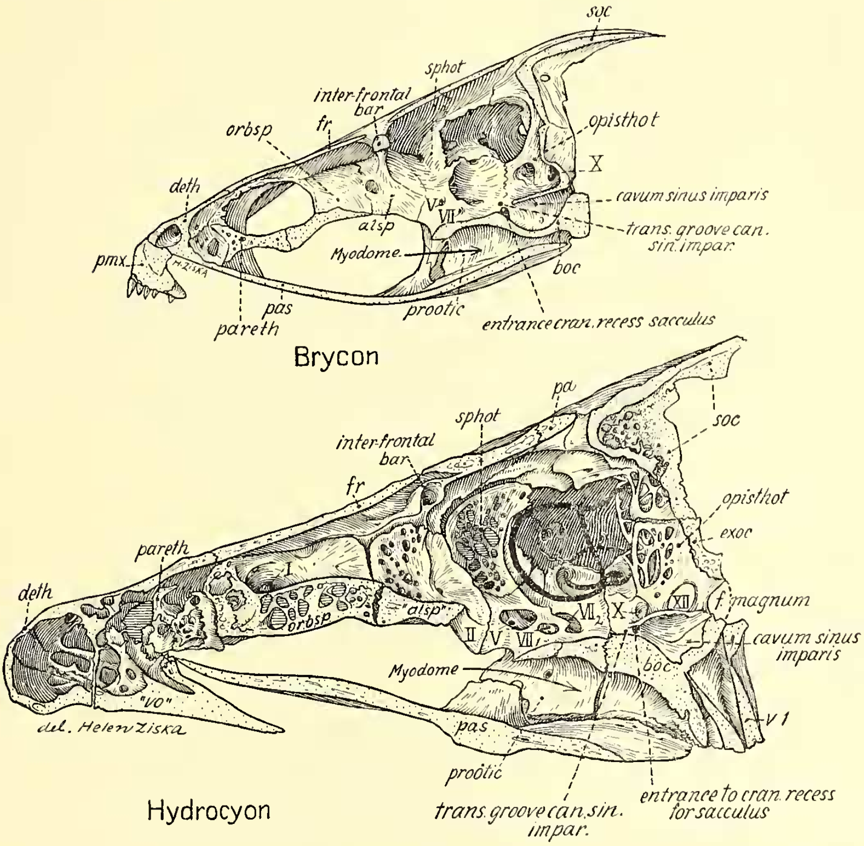
Text-figure 11.

Neurocrania of the African *Hydrocyon* and the South American *Brycon.* The first four vertebrae with their attendant Weberian apparatus are included with the skull of *Hydrocyon.* Although the Weberian ossicles and anterior vertebrae have not been added to the skull of *Brycon,* a close similarity in basic plan of the neurocrania is noted in these two members of the Characinae.

CHARACINAE.

This group is the most extensive of the family, abounding as it does in both South American and African forms which range from the primitive African genus, *Alestes,* to the South American fresh-water flying fish, *Gasteropelecus.* Although the interrelationships of the group are obscure and are in the sense used by Eigenmann (1917) probably polyphyletic, there is little doubt that they are all traceable to the completely primitive Cheirodontinae. The Characinae include on our chart (Text-fig. 2) as representatives of the group, the following genera:

(A) American
Brycon
Diapoma
Corynopoma
Chalcinus
Gasteropelecus



Text-figure 12.

Neurocrania of *Hydrocyon* and *Brycon,* longitudinal sections. These sections show even more strikingly the basic similarity of the African and South American genera of Characinae. The heavy black lines in *Hydrocyon* indicate the position of the semicircular canals.

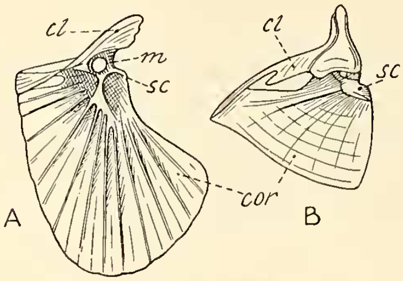


Fig. 13

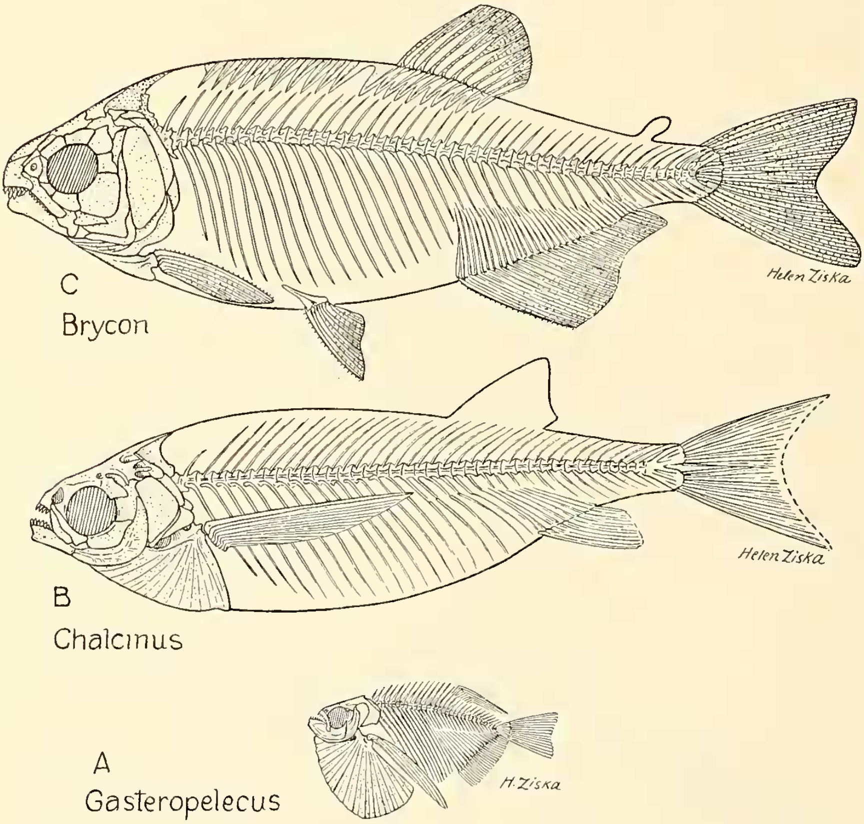


Fig 14

Text-figure 13 (upper).

Cleithrum and primary pectoral arch (except radials) of A. *Gasteropelecus pectorosus* and B. *Chalcinus trachypomus*. After Regan, 1911.

Text-figure 14 (lower).

Skeletons of *Gasteropelecus, Chalcinus* and *Brycon*.

(B) African

Alestes
Hydrocyon

This group may be split into several series, all of which seem to be ultimately derivable from cheirodont beginnings. The African members are closely related to their South American allies in the fundamental pattern of skull structure (Text-figs. 11, 12) as well as in many curious details of body form, scalation, etc.

According to Eigenmann the Glandulocaudinae, here represented by *Diapoma* and *Corynopoma* (Text-fig. 2), are linked quite definitely to the Cheirodontinae by *Paragoniates*, with its general shape and backward position of the dorsal fin, and by *Compsura* and *Odontostilbe*, with the peculiar caudal scalation of the males.

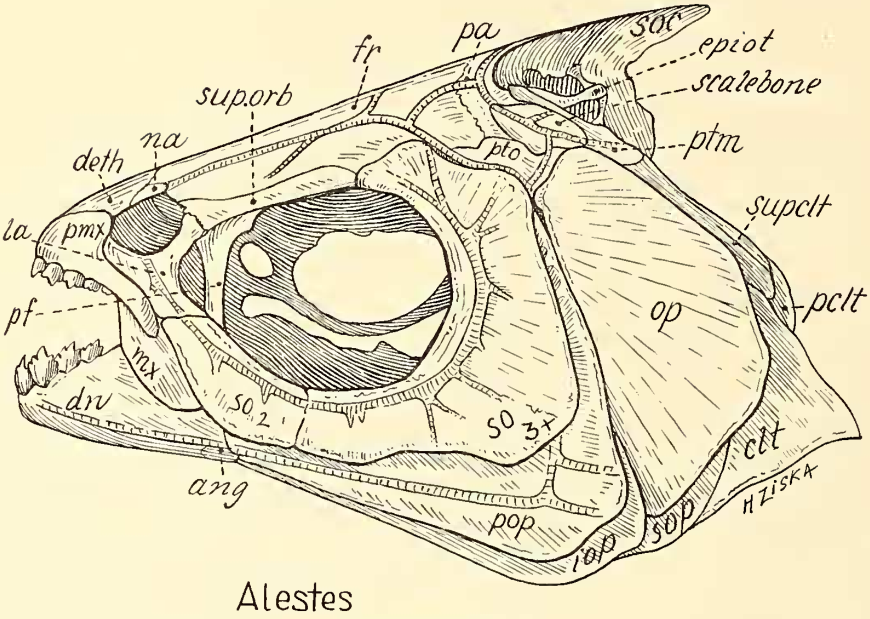
Brycon (Text-figs. 2, 9) seems to be the central type of the group and from it, according to Eigenmann (1917), arose one line leading to *Iguanodectes* and *Pyrrhulina*. Eigenmann and Myers (1929) describe the subfamily Iguanodectinae as "slender, elongate, moderately compressed, smelt-like fishes of small size . . ." Cockerell (1913) remarks that the iguanodectine scales are not far from the condition noted in *Cheirodon*. *Pyrrhulina* is apparently near to the point at which the hemiodontines branched from the cheirodont stem.

Chalcinus (Text-fig. 2), in its deepened coracoids and large pectoral fins, seems to afford a favorable point of departure for *Gasteropelecus* (Text-fig. 2). Regan (1911, p. 20) rejected this connection and stressed the structural relationships with *Tetragonopterus*. But the latter differs widely from *Chalcinus* (Text-fig. 14B) in the low position of the pectorals, general form of body and mouth, and undoubtedly points rather to *Serrasalmo*. After comparing the skeletons of *Chalcinus* and *Tetragonopterus* with the skeleton of *Gasteropelecus* (Text-fig. 14A), we incline to the opinion that *Chalcinus* is much the nearer to the structural ancestor of *Gasteropelecus*.

Alestes (Text-figs. 2, 10), a relatively primitive predator, is typical of several African members of the Characinae, such as *Bryconaethiops*, *Micralestes*, and *Petersius*, which vary from fusiform to fairly deep-bodied shapes. The teeth vary from very small pluricuspid to large compressed shearing types; some even have molar-like teeth on the inner row of the upper jaw.

That the African genus *Alestes* is surely close to the American *Brycon* is undoubted. The general shape of the skulls (Text-figs. 15, 16) is very much alike. They both possess the supraorbital, but whereas *Brycon* retains the dermosphenotic, it is noteworthy that in *Alestes* the frontal is excluded from the orbit by a prolongation of the suborbitals. However, in *Alestes* the dermosphenotic may be so completely fused with the suborbitals as to be indistinguishable from them. At any event, the postorbital portion of the circumorbital chain serves the purpose of protecting the muscle fossae noted in Text-fig. 8, as does the dermosphenotic when present. In both genera the lacrymal is present (not shown in Text-fig. 14) and well separated from the parethmoid, as in primitive characins.

Hydrocyon (Text-figs. 17, 18) is an extreme predaceous, pike-like offshoot of this African stock. Regan (1911) separates it as a distinct subfamily from the rest of his Characidae largely on the basis of the movable premaxillae, but this character is developed independently in other groups of characins (e.g., Anostomatinae, Hemiodontinae, Citharininae and Distichodontinae) and should not outweigh the many marks of close kinship with other African Characinae. If we are to grade taxonomic rank according to intensity of specialization then the complex symphysial hinge-joint of *Hydrocyon* (Text-figs. 19, 20, 21) should entitle it to the grade perhaps of a superfamily. However, other characins (Text-fig. 22) and even its own



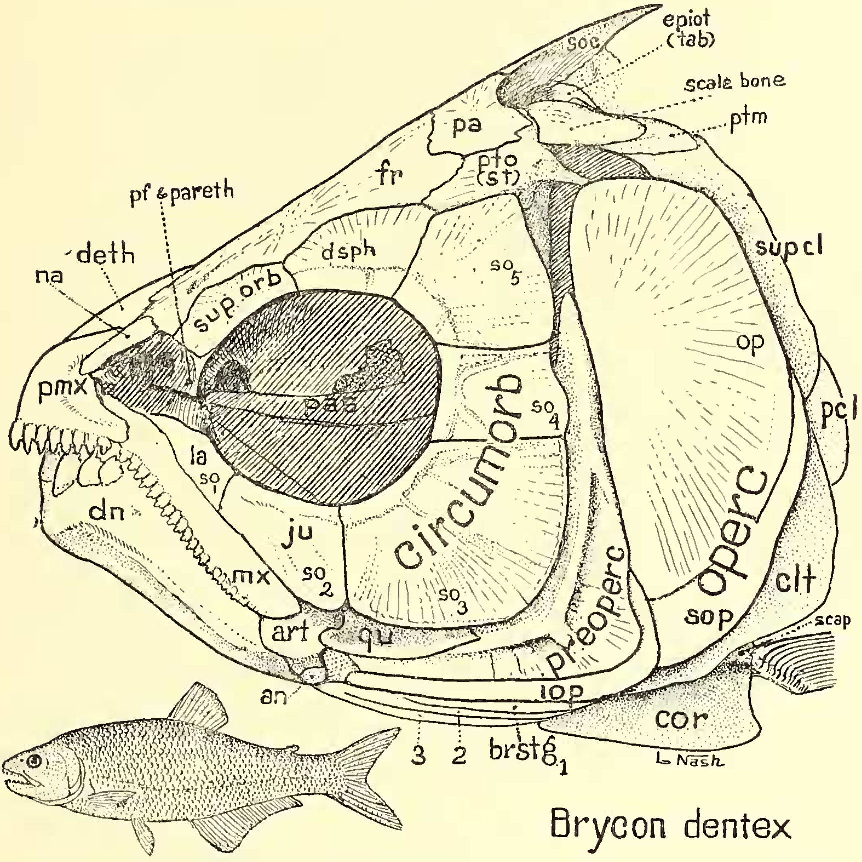
Text-figure 15.
Skull of *Alestes*.

young clearly point the way toward the complex hinge-joint of *Hydrocyon*.

The complex symphysial hinge-joint of *Hydrocyon* and other characins is described in more detail by Gregory and Conrad (1936) as follows:

"Thus the story of the development of the complex hinge-joint in *Hydrocyon lineatus* starts at a stage when the 'hinge' is nothing more than an interdigitating articulation with but three knuckles to each dentary [Text-fig. 21, I.]. The dorsal border of the dentary then produces another knuckle, *C*, on the right and *b* on the left. The ventral border of the left dentary gives rise to *f* [Text-fig. 21, II.]. The next stage [Text-fig. 21, III.] sees the first advance toward the adult interlocked hinge for, as pointed out above, the knuckles begin to curl from the posterior to the anterior borders of the dentary, leaving an opening or fenestra at the pivotal point. By inserting here an hypothetical phase in which this forward curling is wholly finished and the knuckles are interdigitated, it can be seen that by the coalescence of the knuckles arising from the same dentary the condition in IV. [Text-fig. 21] would occur. Now all the elements are present [Text-fig. 20, V.; Text-fig. 21, IV.] and the left hinge-stop is completely formed, while the right one is in process of coalescence. Finally, in VI. [Text-fig. 20] the hinge-joint reaches its completely formed complex condition, which will with later growth be pulled out and distorted both vertically and horizontally, while at the same time retaining its mechanical efficiency.

"A glance at [Text-fig. 22] shows that the most common condition of the hinge in Characins is that seen in *Moenkhausia* (*Tetragonopterinae* Eigenmann), *Piaractus* (*Mylinae* Eigenmann), and *Alestes* (*Characinae* Regan). In all of these the knuckles are arranged in planes radiating posteriorly from the anterior border of the dentary. Our detailed studies on the family suggest that *Hydrocyon* has evidently arisen from an *Alestes*-like ancestor, and a comparison between the *Alestes* hinge in [Text-fig. 22] and that of *Hydrocyon* in [Text-fig. 21] (II.) shows that the latter passes

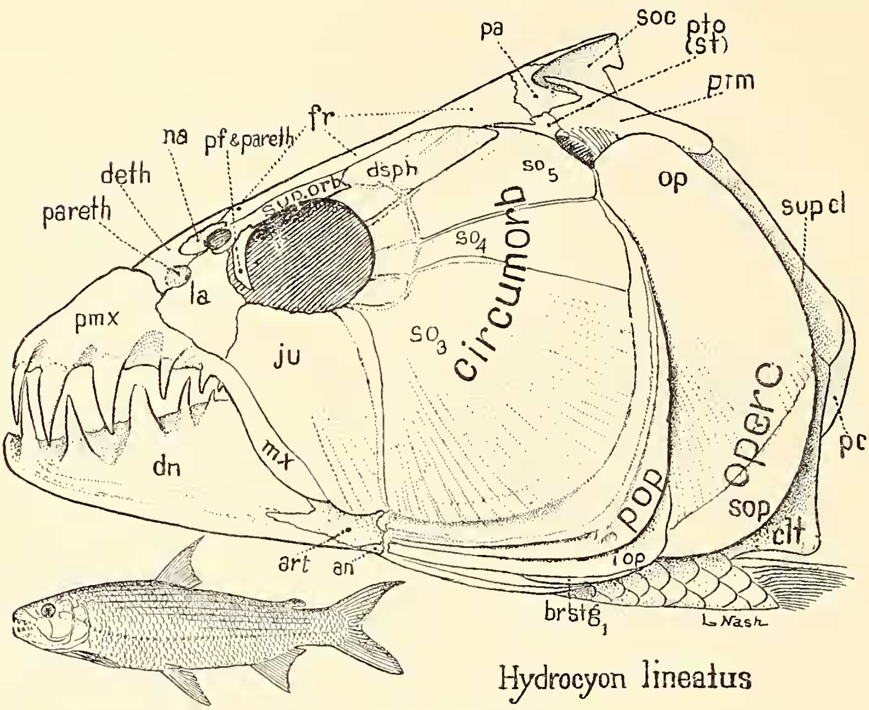


Text-figure 16.
Skull of *Brycon.* After Gregory, 1933, fig. 70.

through an *Alestes* stage in development. Returning to [Text-fig. 22] we notice that the primitive hinge condition is upset in *Erythrinus* and *Hoplias* which have moved the 'area of radiation' posteriorly, so that the knuckles radiate both anteriorly and posteriorly. The condition in *Erythrinus* may possibly be that of *Hydrocyon* in [Text-fig. 21] (IV.) just before any of the knuckles have coalesced.

"In conclusion, the complex hinge-joint in the symphysis mandibulae of *Hydrocyon lineatus* Bleeker develops its most complex features, the so-called hinge-stops described above, after the post-larval and infantile stages have been completed.

"The hinge is formed from interdigitating processes analogous to the knuckles of a mechanical hinge. These knuckles represent subdivisions of the subalveolar ridge of the dentary bone. They are typical polyisomeres in the sense defined by one of us (Gregory, 1934). They grow inward toward the mid-plane like fingers, decussate across the mid-plane, and curl around and join themselves into the hinge-stops on either side of the mid-plane. Here they behave like typical anisomeres, which arise by the differential growth and fusion of polyisomeres.



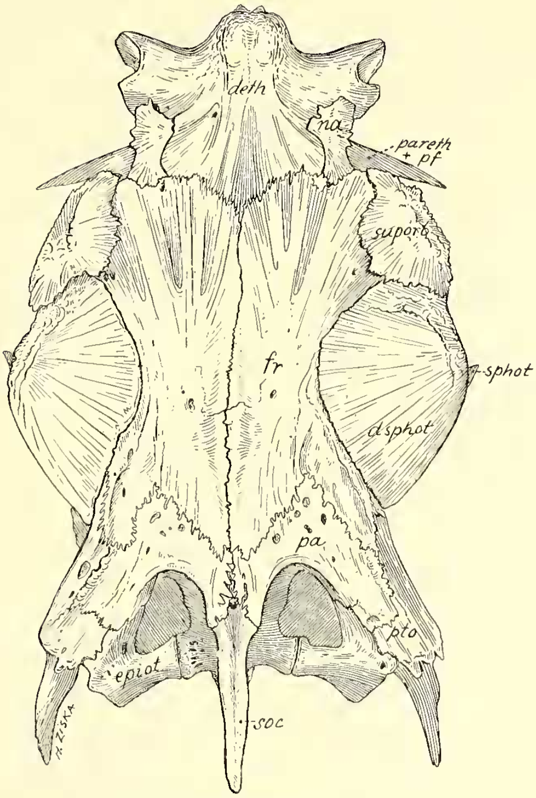
Text-figure 17.
Skull of *Hydrocyon.* After Gregory, 1933, fig. 69.

"The earlier structural stages of the condition in *Hydrocyon* are found in *Alestes* and other primitive Characins and in an arrested stage in the subfamily *Erythrininae.*"

SARCODACINAE.

Acestrorhyncus, with its comparatively long jaws and with its premaxillaries fixed and firmly attached to the mesethmoid, has apparently given rise to the elongate, pike-like Xiphostomatidae of Regan (represented on our chart (Text-fig. 2) by *Acestrorhyncus* and *Luciocharax*).

The similarity of the skulls of *Sarcodaces* (Text-figs. 23, 24), an African form, and *Luciocharax,* a South American, is amazing. Text-figure 23 shows the dorsal views of these skulls. It is seen that the dorsal fontanelle is completely closed over in both and that a triangle is formed by the dermosphenotics, frontals and pterotics. This wedge-like arrangement of the cranial elements is highly suggestive of relationship, coupled as it is with a well developed prefrontal plus supraorbital which is so rare among the other characins examined. The scale bone is not figured in *Luciocharax.* There is no supraopercular bone in *Luciocharax,* but this is a derm bone which might easily be lost. As seen in side view (Text-fig. 24) the two skulls are likewise comparable, with their plate-like lacrymals which are so different from those of the more primitive characins. The prefrontals lie dorsal to the lacrymals instead of behind them as in more generalized forms. The suborbital bones of both are very similar in cut, the bones marked so2 being strikingly alike. There is a persistence of the dermosphen-

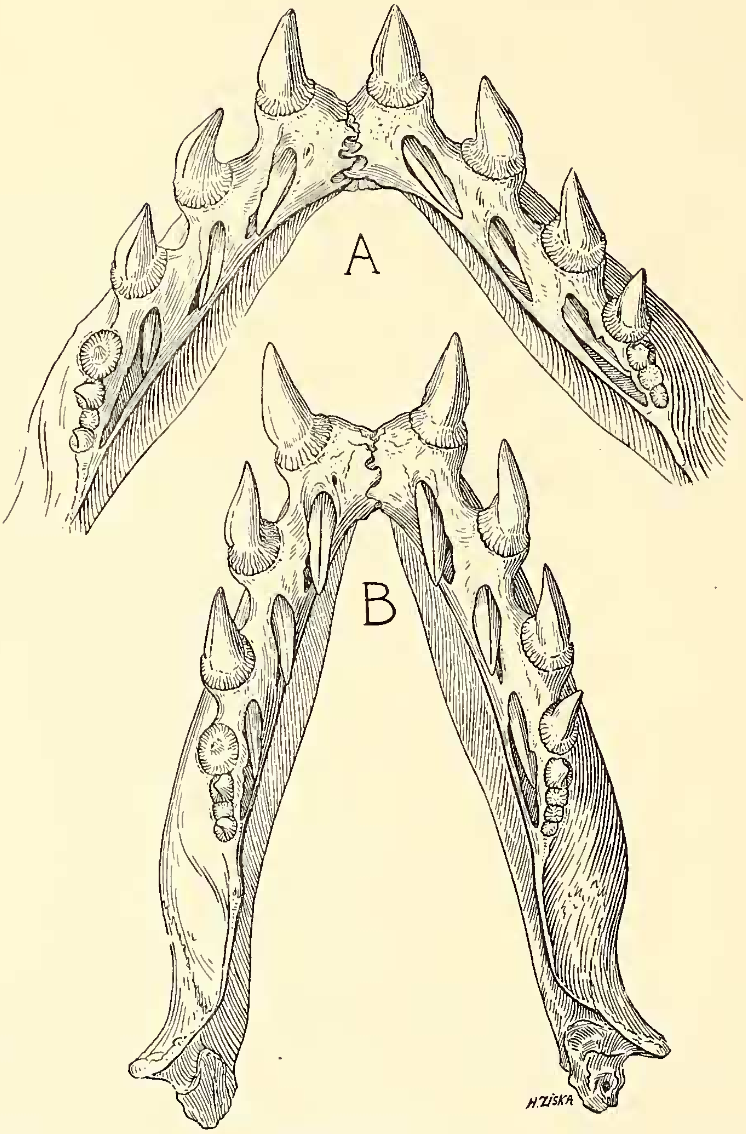


Hydrocyon

Text-figure 18.
Skull of *Hydrocyon*, dorsal view.

otics of the primitive characin. The cut of the operculum is quite similar in both. The premaxilla and dentary of *Luciocharax* have been elongated and the maxilla is somewhat reduced. That the increased number of teeth in *Luciocharax* is secondary is highly probable.

The similarity of these two is so great that it seems warranted to refer *Sarcodaces* to the Sarcodacinae (which includes *Luciocharax* and others) as here understood (page 321). The connection of *Sarcodaces* with *Alestes* and allied genera seems much more remote than with *Luciocharax*. In *Sarcodaces* the lacrymal and prefrontal overlap, as they do in *Luciocharax*, whereas in *Alestes* which has the typical characin lacrymal placement, they are well separated from the parethmoid-prefrontal complex. A supraorbital is present in *Sarcodaces* and *Luciocharax* and is also present in *Alestes*. *Alestes* lacks the dermosphenotic that is present in the others. The general heavily armored character and the telescoped occipital region common to *Sarcodaces* and *Luciocharax* is lacking in *Alestes* and the *Characinae* generally. The large, well developed circumorbitals of *Sarcodaces* are noted in *Hydrocyon*, but the lacrymal and parethmoid are well separated in the latter. *Hydrocyon* has a well developed supraorbital but at the same time retains the dermosphenotics of the primitive *Cheirodon*. The supraopercular found in some few characins, such as *Sarcodaces*, is lacking in *Hydrocyon*. The



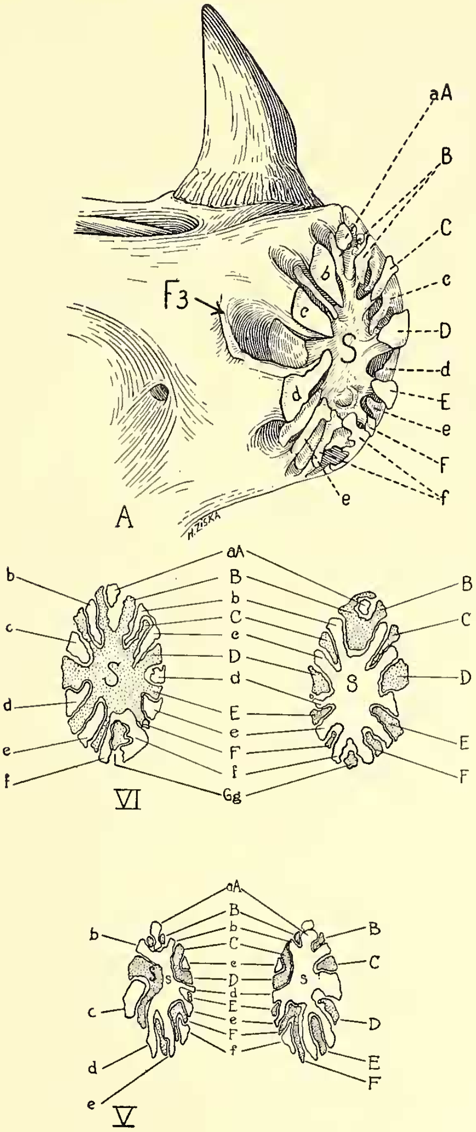
Text-figure 19.

Lower jaw of *Hydrocyon lineatus*, showing the dentaries spread to greatest extent in A and closed as tightly as possible in B. After Gregory and Conrad, 1936, fig. 1.

supraoccipital is produced sufficiently far back to include *Hydrocyon* among the more central Characinae.

Luciocharax, while it retains most of the osteological characters of the Characidae of Regan, has developed a somewhat movable upper jaw and the maxillaries have become firmly united with the premaxillaries.

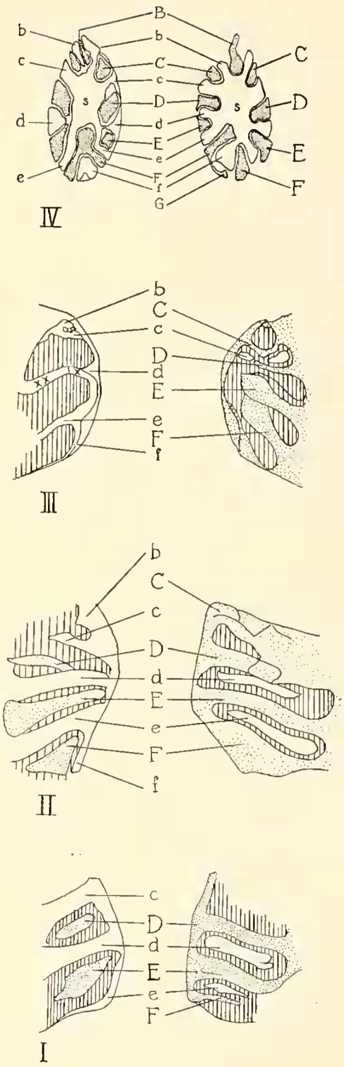
The scales of the Acestrorhamphinae (our Sarcodacinae) according to Cockerell (1913) are like those of the Serrasalmoninae. However, this prob-

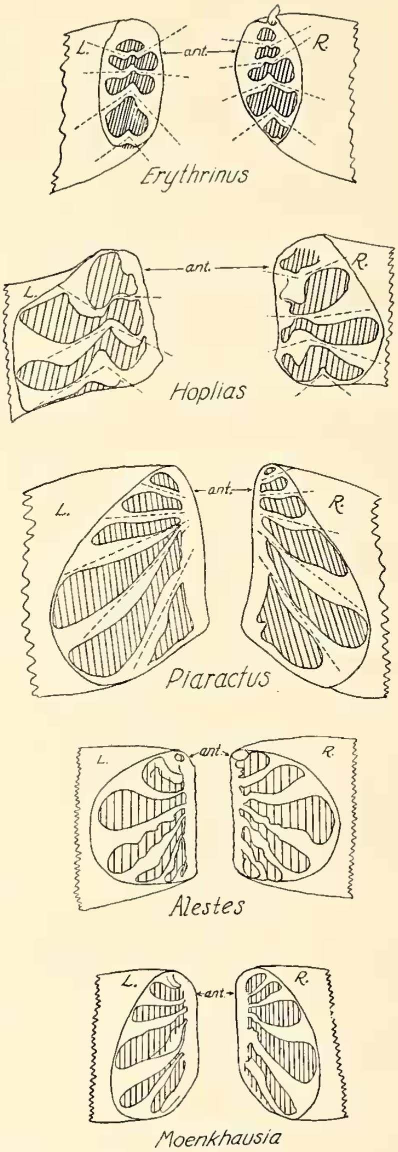


Text-figure 20.

A, distal portion of left half of mandible of adult *Hydrocyon*, oblique mesial view of S turned slightly. VI, median sagittal section of same specimen. V, section of a much smaller specimen, measuring 23 cm. (Stippled portion represents right dentary; unstippled, left.) After Gregory and Conrad, 1936, fig. 6.

ably indicates only a community of origin for the two groups have developed into as many diverging types. While the Serrasalmoninae have become increasingly deep-bodied as noted above, the sarcodacines have been pulled out antero-posteriorly to form, in *Luciocharax*, an astonishingly pike-like fish. Thus the Sarcodacinae like the Serrasalmoninae may be traced back to the Cheirodontinae.





Text-figure 21 (left).

Median sagittal sections of symphysis in *Hydrocyon lineatus*. IV, a specimen about 21 cm. long; III, a fish about 5.5 cm. in length; II, a specimen 5 cm. long; and I, about 2.5 cm. long. After Gregory and Conrad, 1936, fig. 7.

Text-figure 22 (right).

Diagrams of disarticulated symphysial hinges in various characins; mesial views. The hatched portion represents the cavities and the light, the knuckles. The dotted lines are merely an aid in noting the directions of the knuckles. L, left dentary; R, right dentary; ant., anterior border of the dentary. After Gregory and Conrad, 1936, fig. 5.

ERYTHRININAE.

As noted above the primitive appearance of the Erythrininae is apparently only secondary. In a study of the visceral anatomy of the characins Rowntree (1903) notices the striking resemblance between the Erythrininae and *Sarcodaces,* "not only in cranial characters, as shown by Sagemehl, but also in certain visceral characters, notably in the opening of the ductus pneumaticus far to the left on the alimentary canal, in the character of the ovaries, and in the features of the air-bladder." This asymmetric position of the ductus pneumaticus is, according to Rowntree, a specialized condition inasmuch as a symmetric or mid-dorsal position of the duct is the primitive one. That Rowntree and Sagemehl noted several points common to the Erythrininae and *Sarcodaces* is an interesting observation for, of all the skulls studied, the only ones forming possible links between the Erythrininae and the remainder of the Characinidae are those of *Sarcodaces* and related genera.

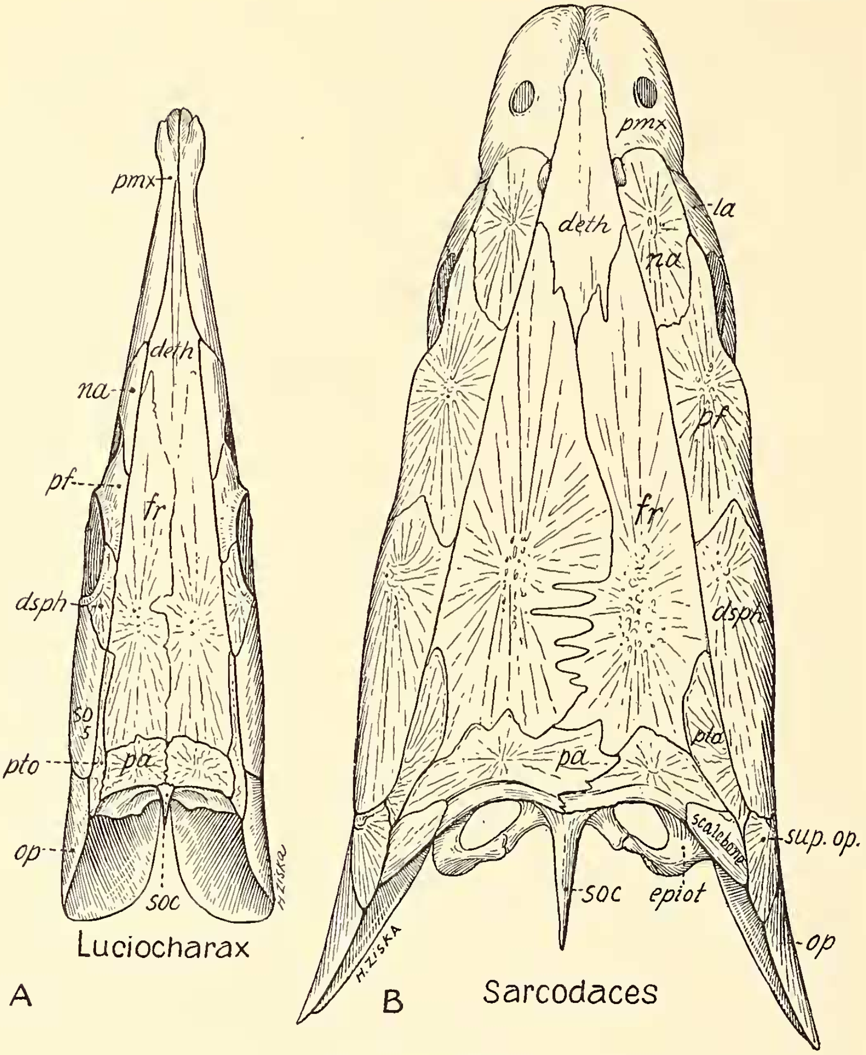
Rowntree further notes that *Macrodon* (*Hoplias*), alone among the Characinidae, possesses but two of the usual three liver lobes. Insofar as scales are concerned Cockerell (1913) shows that the Erythrininae combine characters of the characins and cyprinids.

Studies on the symphysial hinge-joints in characins seemed to indicate at first that the condition noted in *Erythrinus* (Text-fig. 22) was a precursor of that found in *Hydrocyon.* Upon further consideration (see above, page 337), however, it is more probable that the *Erythrinus* condition of the symphysial hinge-joint is merely that of *Hydrocyon* in an arrested stage.

In any event it becomes evident that the Erythrininae are well along in the evolutionary series, but in spite of their amazing similarity to the cyprinids in the scales it is doubtful that they are near to the stem leading from the primitive Ostariophysi to that group. The well developed upper and lower jaws are armed with conical, canine-like teeth much as in *Sarcodaces* (Text-fig. 24). The condition of their jaws and teeth and the lack of an adipose fin are early noted in the cheirodont *Grundulus,* and the *Erythrinus* body-form has been developed time and again within the family Characinidae.

The heavily armored, tightly built skull of the Erythrininae (Text-figs. 24B, 25, 26) closely resembles those of the Sarcodacinae. *Hoplias* (Erythrininae) (Text-fig. 24B), with its elongate dermosphenotic and separate supraoperculum, seems to form a connecting link between *Sarcodaces* and *Erythrinus.* The lacrymal and the pre-fronto-parethmoid articulate in this subfamily and are not separated from each other as they are in more primitive characins. However, the Erythrininae resemble the primitive subfamilies in not having the frontal excluded from the orbit, whereas in *Sarcodaces* and *Luciocharax* the enlarged prefrontal plus supraorbital do exclude the frontal from the orbital margin. Both *Erythrinus* and *Sarcodaces* have large nasals. The interfrontal sutures and the sutures between the parietals are very similar in the two, but *Erythrinus* lacks the characteristic triangular dorsal view in *Sarcodaces.* The fontanelles are entirely covered over in both genera. The dentition of *Hoplias* is quite like that of *Sarcodaces.* The cut of the lower border of the operculum in the Erythrininae and *Sarcodaces* is peculiar, but this is approached also in *Curimatus* (Anostomatinae).

Lebiasina and *Piabucina* (Text-fig. 26), referred by Regan to his Characidae (*sensu strictu*), show a close approximation to *Erythrinus* not only in the body-form but even in the skull. The fronto-parietal fontanelle is completely closed over; the operculum is very similar; the lacrymal-parethmoid relationship is as in the Erythrininae; and there is a sizable dermosphenotic. The only specimen available does not seem to have a supraopercular. The dorsal aspect affords a favorable comparison with *Erythrinus.* The coracoids of *Lebiasina,* according to Regan, have the median



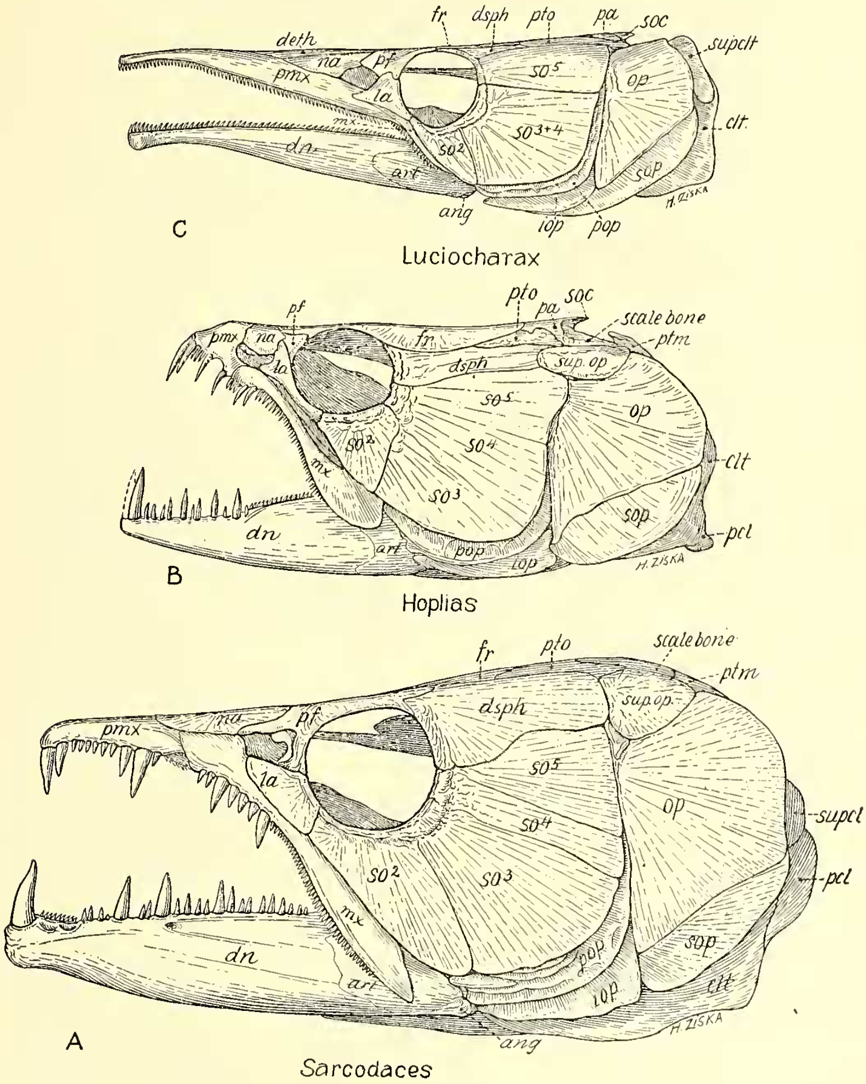
Text-figure 23.
Skulls of *Luciocharax* and *Sarcodaces,* dorsal views.

ventral laminae present but short whereas in the Erythrininae generally these are absent.

Thus the Erythrininae may easily have been derived either from a cheirodont near to the *Alestes-Hydrocyon* stem or from the immediate ancestors of the Sarcodacinae.

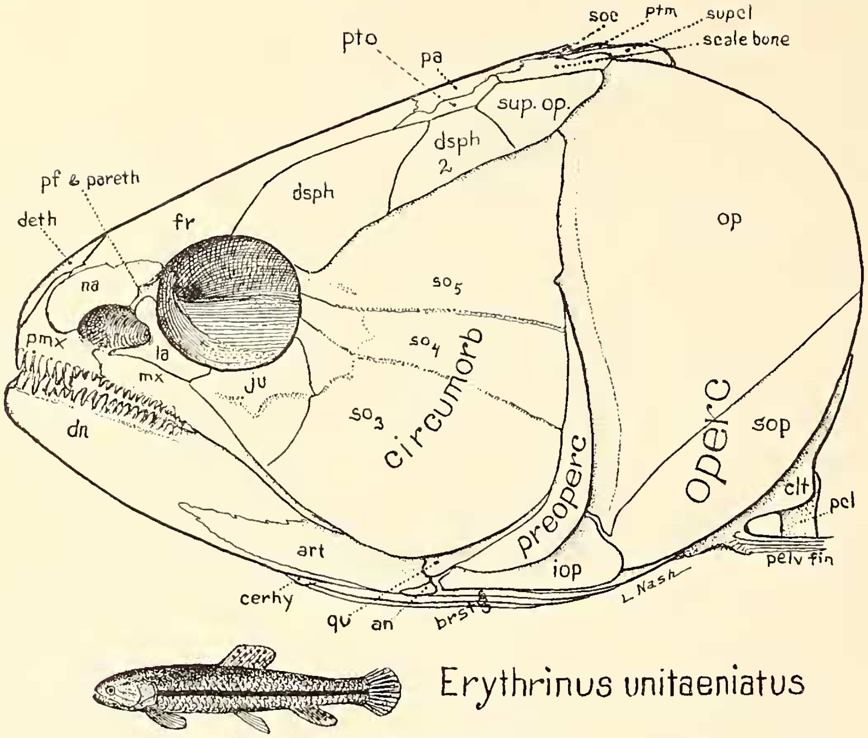
HEMIODONTINAE.

Regan (1911) points out that with the exception of certain diagnostic skull characters, the osteological characters of the Hemiodontinae are "essentially similar to the Characidae." As noted above (p. 321) his "Characidae" has been redefined in part as the Characinae. Cockerell (1913) notes that

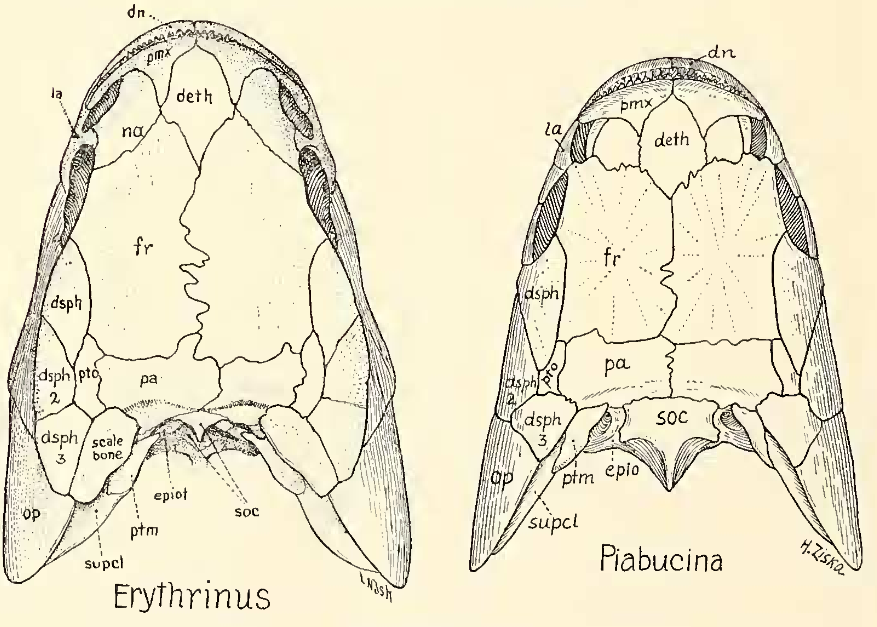


Text-figure 24.
Skulls of *Sarcodaces, Hoplias* and *Luciocharax*, lateral views.

the scales of the "Pyrrhulinae," which we refer to the Characinae, are very similar to those of *Nannostomus* of the subfamily Hemiodontinae. On the other hand Cockerell states that the scales of *Hemiodus, Anisistsia* (Hemiodontinae), and *Anostomus* (Anostomatinae) are of the curimatine type (*Curimatus* being referred by us to the Anostomatinae), while the scales of *Poecilobrycon* (Hemiodontinae) and *Nannostomus* (Hemiodontinae) are like those of *Leporinus* (Anostomatinae), indicating for the hemiodontines a position close to the anostomatine series. However, because of the slight affinities of *Pyrrhulina* and other members of the Characinae to the Hemiodontinae we consider the subfamily Hemiodontinae as a side



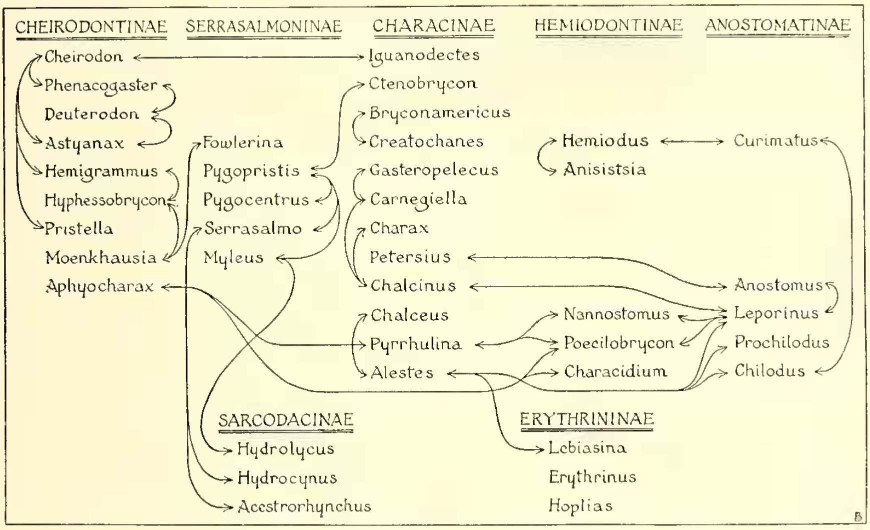
Text-figure 25.
Skull of *Erythrinus*, lateral view. After Gregory, 1933, fig. 67.



Text-figure 26.
Skulls of *Erythrinus* (after Gregory, 1933, fig. 68) and *Piabucina*, dorsal views.

shoot of the *Cheirodon-Curimatus* line. *Parodon* (Hemiodontinae) with its rather short body seems to be a primitive forerunner of the elongate, fusiform *Poecilobrycon* (Text-fig. 2). The Hemiodontinae and Prochilodinae of Regan both have a single headed hyomandibular in contrast to the double headed condition seen in the remainder of the family.

The subfamily resemblances between the scales of various genera as observed by Cockerell (1913) may, according to our classification, be tabulated as in Text-fig. 27.



Text-figure 27.

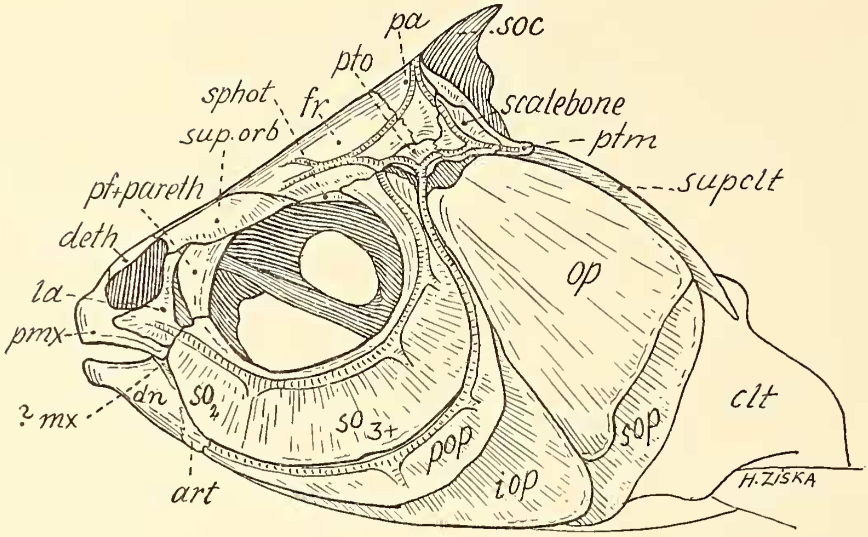
Resemblances between the scales of various genera of characins as noted by Cockerell, 1913.

ANOSTOMATINAE.

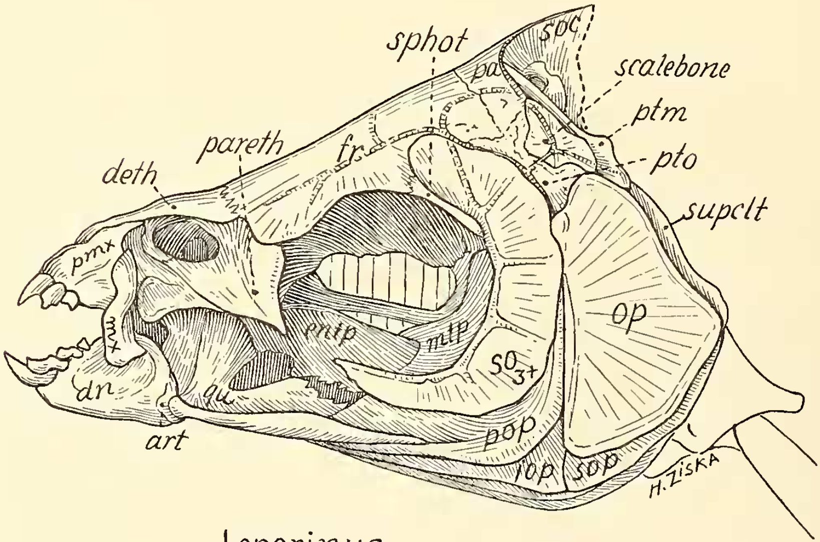
The Anostomatinae, a rather compact group, are represented in the "Pictorial Classification" (Text-fig. 2) by *Anostomus, Prochilodus, Chilodus* and *Curimatus*. The series starts with *Anostomus*, which possesses a small, non-protractile mouth and has the rami of the lower jaw short and stout. *Leporinus* is very close to *Anostomus;* it is said by Cockerell (1913) to have curimatoid shaped scales with a very definite alestoid relationship. *Chilodus* also has scales of curimatoid shape with evidence of a part of the alestiform pattern. Cockerell goes so far as to state the belief that this group supplies the link between *Distichodus* and *Alestes* because their scales undoubtedly illustrate the beginning of the development which culminates in the specialized ctenoid scales of the African *Xenocharax*. In *Prochilodus* we have at last a real development of the ctenoid scale, combined with an alestoid radial pattern. It is apparent from scale studies that *Prochilodus* leads us toward a separate offshoot of the curimatoids, possibly to the African distichodonts, but certainly near and parallel to them.

The curimatoids proper are represented in our "Pictorial Classification" by *Curimatus*. This toothless form constitutes the "end-genus" of this line of divergence from the Cheirodontinae.

As a whole the subfamily Anostomatinae is highly specialized and far from its original ancestor, a generalized cheirodont. These conclusions con-



Curimatus

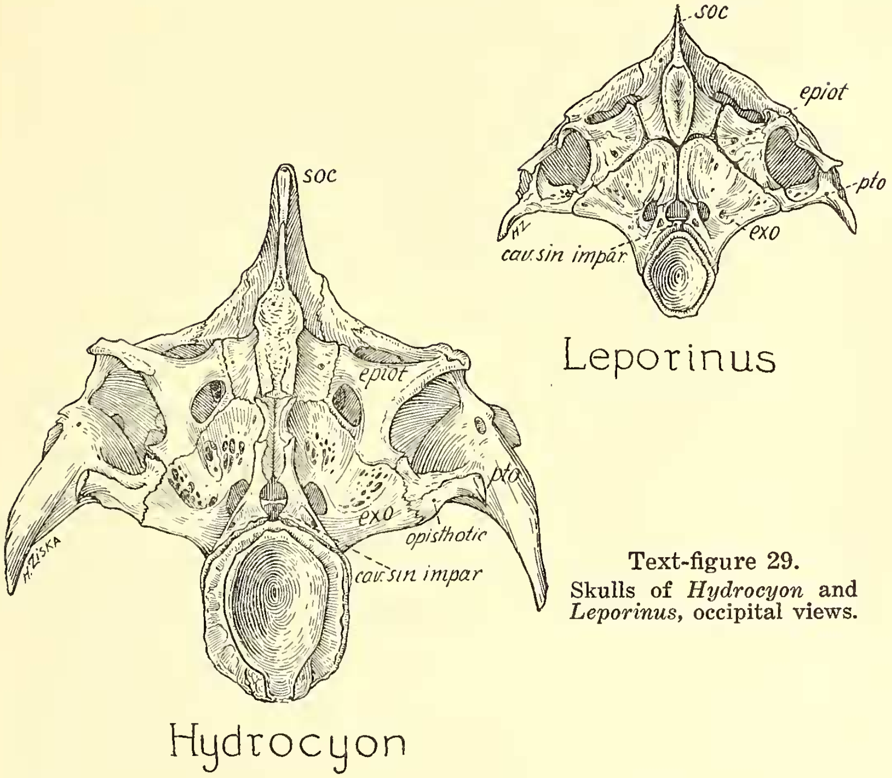


Leporinus

Text-figure 28.
Skulls of *Leporinus* and *Curimatus.*

cerning the relationships of this group, based largely upon scale structure, are in accord with Eigenmann's systematic studies (1917).

The skulls of this group that we have been able to study are *Curimatus* and *Leporinus* (Text-fig. 28). A supraorbital bone is present in *Curimatus* and *Prochilodus* but is absent in *Leporinus.* The fontanelle in both *Curimatus* and *Leporinus* completely separates the frontals from the occiput



Text-figure 29.
Skulls of *Hydrocyon* and *Leporinus*, occipital views.

to the dermethmoid; the lacrymal and parethmoid are well separated; the supraoccipital is produced posteriorly; the maxilla is greatly reduced, the small nibbling jaws retain strong teeth in *Leporinus* but are edentulous in *Curimatus* and some others. The lower border of the operculum in *Curimatus* is truncate postero-inferiorly as in *Sarcodaces*. The opercular region of the skull extends postero-ventrally in *Curimatus* but to a much lesser degree in *Leporinus*.

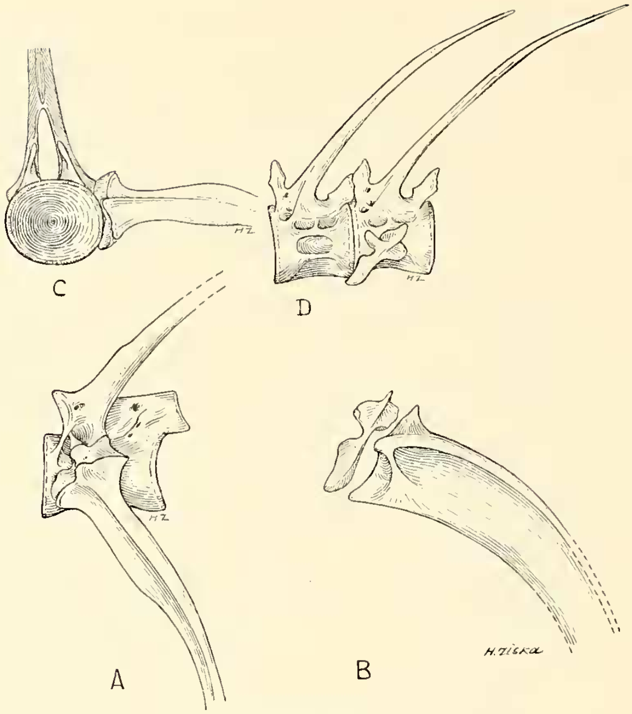
Text-figure 29 shows the great similarity between the occipital regions of the skulls of the African characine, *Hydrocyon*, and the South American anostomatine, *Leporinus*.

The implied relationship on the chart (Text-fig. 1) between the Anostomatinae and the Citharininae is strengthened by the skulls. It may be, however, that these resemblances are merely due to parallelism for both subfamilies reflect their cheirodont ancestry.

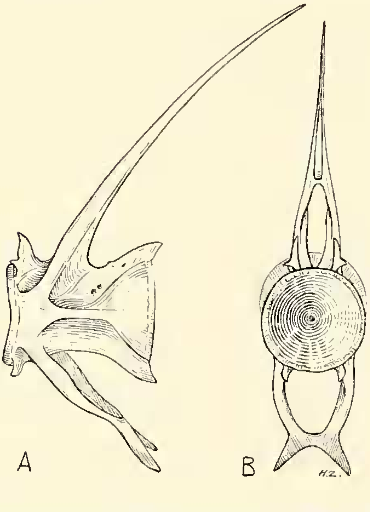
The ribs of *Leporinus* and other genera, along with those of the remainder of the Characinidae, are articulated to the centrum by autogenous parapophyses. Text-figures 30, 31 give front and side views of vertebrae in the abdominal and caudal regions. Text-figure 32 shows the arrangement of the hypurals in *Leporinus*.

CITHARININAE.

Regan (1911) refers the African *Citharinus* (Text-figs. 2, 3) and its ally *Citharidium* (Text-fig. 3), along with many other African genera, to

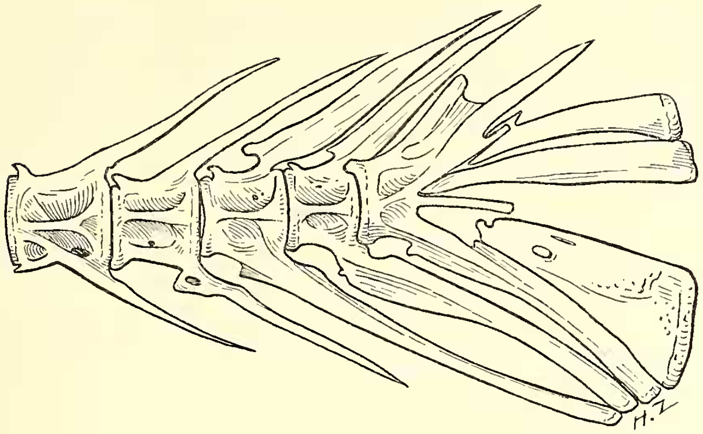


Text-figure 30.
A, C, side and front views of abdominal vertebra of *Leporinus*, showing rib and autogenous parapophysis. B, autogenous parapophysis and rib of *Brycon;* D, with autogenous parapophysis attached to centrum in *Brycon.*



Text-figure 31.
A, lateral view and B, front view of caudal vertebra in *Leporinus.*

the family Citharinidae. We, however, prefer to segregate *Citharinus* and *Citharidium* and their near allies, *Nannaethiops, Neolebias, Xenocharax* (Text-fig. 3), *Hemistichodus,* in a more primitive subfamily, Citharininae,



Text-figure 32.
Arrangement of hypurals in *Leporinus.*

characterized by the absence of the high specializations of the mouth parts seen in the Distichodontinae, as here understood.

Boulenger in the Cambridge Natural History, places both *Prochilodus* (Text-figs. 2, 3), a definitely ctenoid South American anostomatine, and *Curimatus* (Text-figs. 2, 3) in the Citharininae; nor was this classification wholly unwarranted, for his conclusions are supported by other anatomical features, i.e., both have movable upper jaws, premaxillaries articulating on the mesethmoid, maxillaries articulated with or adherent to the premaxillaries, palate toothless, lateral line straight, etc.

Cockerell (1912) separates the scales of the African subfamily Citharininae into the *Citharidium* type and the *Citharinus* type, the former with ctenoid and the latter with cycloid scales. It is evident that *Citharinus* with the more primitive cycloid scale is the forerunner of the ctenoid *Citharidium.*

The skull of *Citharinus* compares rather well with that of the Anostomatinae, especially *Prochilodus* or *Curimatus* (Text-fig. 28). The similarity and extent of the fontanelle and the presence of supraorbital are noteworthy. The jaws, too, are quite similar in both subfamilies.

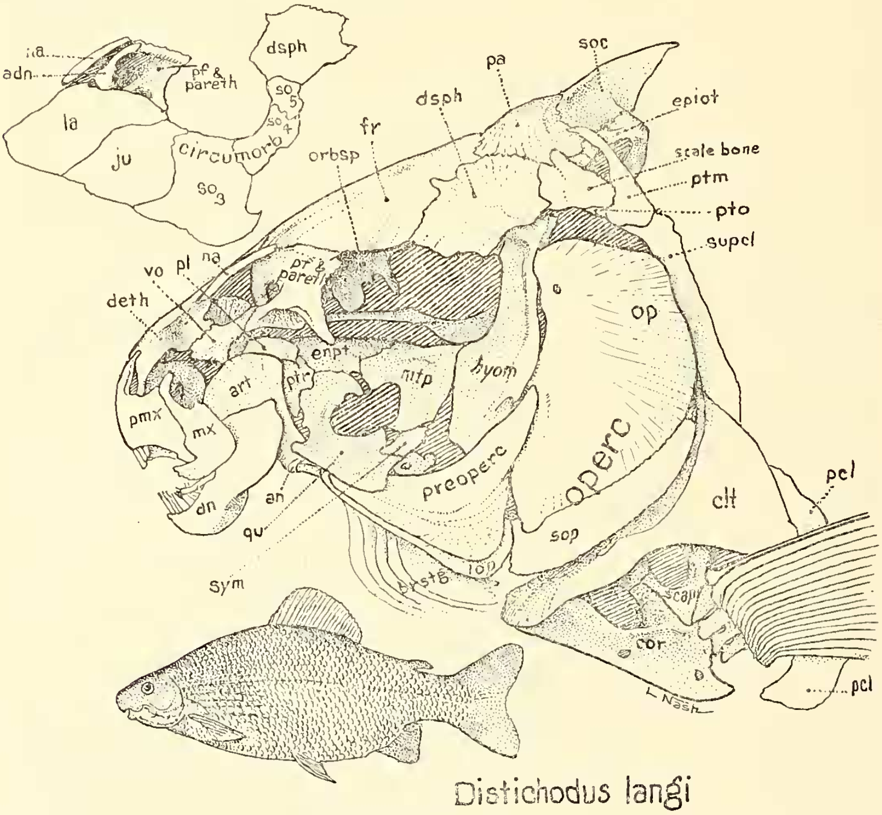
In further support of an early connection between the Anostomatinae and the Citharininae, Rowntree (1903) writes of an accessory branchial organ arising as a blind sac from the upper margin of the last gill cleft; this character seems to be peculiar to the herbivorous forms, *Hemiodus* (Hemiodontinae), *Prochilodus, Caenotropus, Curimatus* (Anostomatinae), and *Citharinus, Xenocharax* (Citharininae). Sagemehl identified this structure as an organ arising from the rudimentary fifth branchial arch. "If this conclusion," says Rowntree, "be correct the presence of the organ in the herbivorous Characinids, and in these only, becomes of great interest, in view of the fact that traces of a fifth gill have not been found in any living ganoid, but only in fishes of yet lower organization—certain Selachians and Dipnoids."

Apparently, however, both Sagemehl and Rowntree failed to realize that selachians and dipnoans have no connection with teleosts and that the so-called fifth branchial arch has no definite claim to be homologized with those of selachians and dipnoans, but is more probably a secondary response to the presence of an accessory branchial organ.

Rowntree then procedes to draw these conclusions, "(1) that the herbivorous Characinids which possess it (the accessory branchial organ) form a natural group; and (2) that this division of the family cannot be derived from either the Erythrinoids or the other carnivorous Characinids, but is at least as ancient as either of these groups." His first conclusion, at least, seems safe and serves as more positive evidence in showing the interrelationship of the anostomine-citharinine group.

DISTICHODONTINAE.

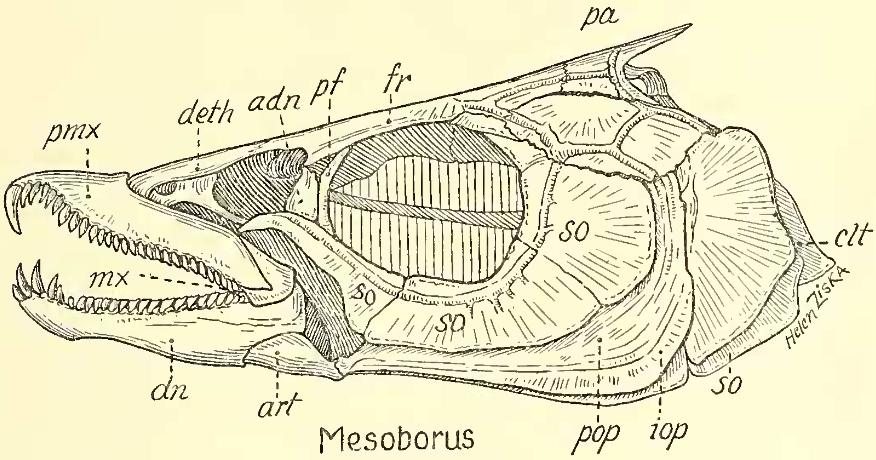
Regan's subfamilies, Distichodontinae and Ichthyoborinae, are closely linked by the possession of more or less massive dentaries, firmly united at the symphysis and *movably articulated with the articulars.*



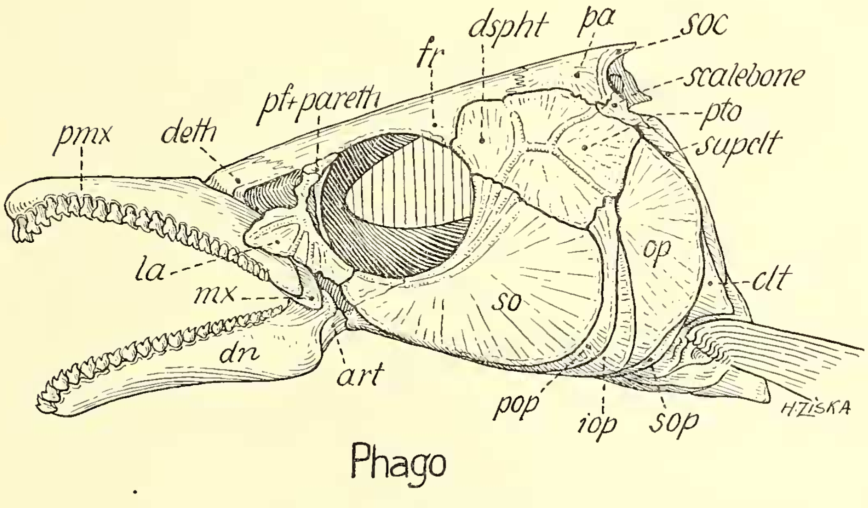
Text-figure 33.
Skull of *Distichodus*. After Gregory, 1933, fig. 71.

That these African forms were derived from the ctenoid African Citharininae seems more likely than that they came from the ctenoid South American anostomatines. Apparently drift toward the herbivorous distichodonts took place in or near the stem of the Anostomatinae and Citharininae (Text-fig. 1).

Distichodus (Text-fig. 33) is apparently more primitive than *Mesoborus* (Text-fig. 34), *Ichthyoborus*, or *Phago* (Text-fig. 35). The lengthening of body and jaws in *Ichthyoborus* and the development of unicuspid teeth are probably secondary conditions as contrasted with the primitive short jawed, deep bodied *Distichodus*. With regard to the scales Cockerell (1912) notes that there is nothing to distinguish the scales of *Ichthyoborus* from those of *Distichodus*.



Text-figure 34.
Skull of *Mesoborus*.



Text-figure 35.
Skull of *Phago*.

GYMNOTIDAE.

To judge from the cranial osteology the gymnotids have probably been derived from some primitive member of the Characinae. The chief habitus specializations are:

(1) Marked forward inclination of the entire suspensorium, primitively correlated with a small projecting mouth;

(2) Varied reduction or emphasis of premaxilla and maxilla;

(3) Reduction and loss of true pterygoid correlated with enlargement of entopterygoid (mesopterygoid) and symplectic;

(4) Loss of parethmoid (prefrontal) and varied reduction of mesethmoid;

(5) Loss of suborbital series including lacrymal;

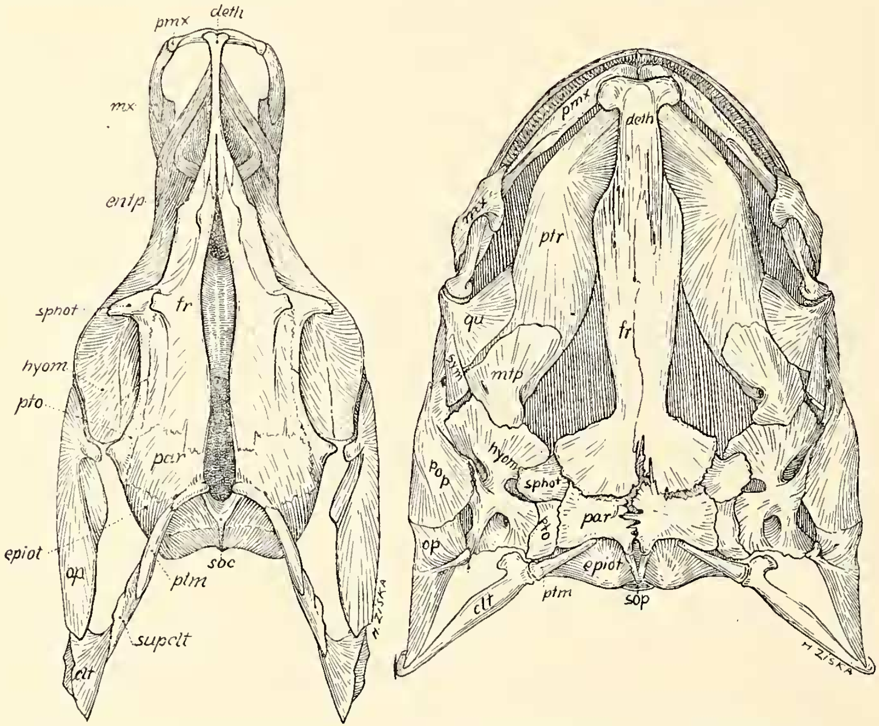
(6) Reduction or loss of postorbital process (dermosphenotic);

(7) Varied emphasis or reduction and loss of interfrontal fontanelle.

Regan has noted that the pectoral girdle of *Rhamphichthys* is much less specialized than that of the typical "Sternarchids." This genus has a greatly elongated, decurved snout with a very small mouth and thus parallels some of the long-snouted mormyrids.

A possible explanation of the peculiar specializations of the gymnotid skull as above noted may be as follows:

All primitive gymnotids being lost, the genus *Rhamphichthys*, even with its "mental vent," may be near the structural starting point for the remaining genera. We have only to suppose that with the extreme elongation of the snout the maxilla lost its normal connection with the reduced

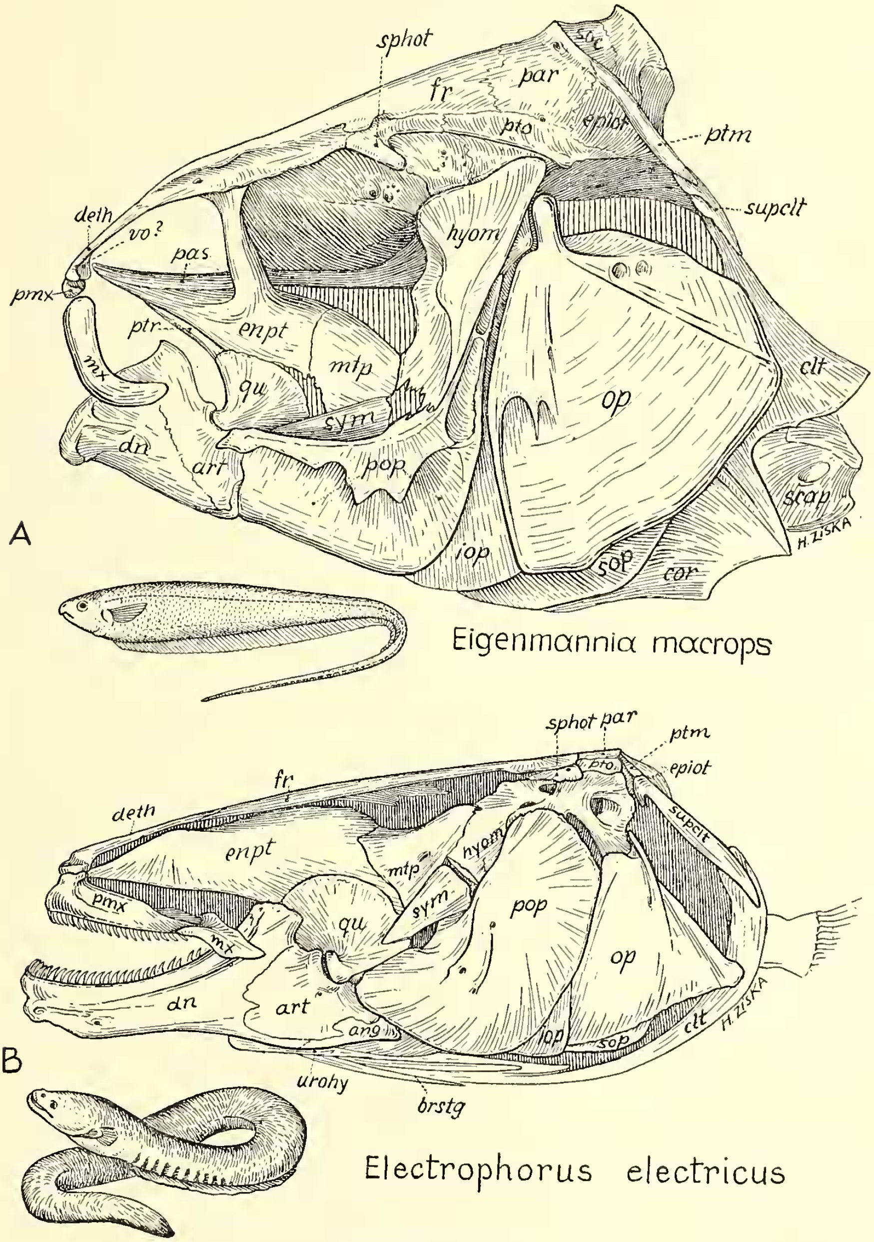


A Eigenmannia macrops B Electrophorus electricus

Text-figure 36.

Skulls of *Eigenmannia* and *Electrophorus*, dorsal views. After Gregory, 1933, fig. 72.

palatine, retaining only its contact with the premaxilla, the latter resting only upon the prolonged mesethmoid. As the palatine disappeared the true pterygoid became reduced and the entopterygoid enlarged. Meanwhile the entire suspensorium was swinging far forward as the mouth became



Text-figure 37.

Skulls of *Eigenmannia* and *Electrophorus*, lateral views. After Gregory, 1933, fig. 73.

smaller and smaller at the end of the lengthening edentulous snout. In the line leading to *Sternarchus* and *Eigenmannia* (Text-figs. 36, 37) a reverse movement then set in involving the secondary shortening of the snout and the *secondary* widening of the mouth which even acquired secondary teeth. The end-stage is *Electrophorus* (Text-figs. 36, 37) in which the mesethmoid is secondarily enlarged and strengthened and the median frontal fontanelle is completely closed to support the upward thrusts of the stout upper and lower jaws. Meanwhile the maxilla, having long since lost its primitive contact with the palatine, remains as a vestigial tab on the distal end of the secondarily enlarged premaxilla.

To those who hold to current interpretations of "Irreversibility of Evolution" such an explanation can only appear fantastic. But if we once grasp the idea of secular rise and recession of specializations the above steps will be seen to be supported by strong morphological evidence as well as by closely analogous series among the long-snouted mormyrids *Gymnarchus* and their secondarily short-snouted relatives, such as *Petrocephalus* (Gregory, 1933, Figs. 62B, 64).

THE CHARACINS AND THE SUPPOSED SOUTH AMERICAN-AFRICAN BRIDGE.

The unique distribution of the Characidae in Africa and South America alone has long engaged the attention of ichthyologists. Africa and South America each serve as subsidiary centers for adaptive radiation of the group, the Cheirodontinae, Serrasalmoninae, Erythrininae, Anostomatinae and Hemiodontinae being characteristic of South America while the Citharininae and Distichodontinae are confined to Africa. The Characinae and Sarcodacinae, however, as here understood, have representatives in both continents and the resemblances between certain African and South American forms are so striking (Text-figs. 9, 10, 11, 12, 22, 23, 24, 29) as to leave a strong impression of close relationship.

Accordingly, the preceeding study leads us to the following tentative conclusions:

(1) that the African and South American characins are closely related;

(2) that so far as known characins are wholly absent from ancient freshwater deposits of North America;

(3) that there is much evidence analyzed by C. W. Andrews, Schuchert and others for the reality of a narrow isthmian land or archipelago connecting Brazil with West Africa even in possibly late Tertiary times.

Dr. Bequaert, however, in the light of his wide knowledge of the faunae and florae of South America and Africa, tells us that neither the botanists nor the entomologists would favor the assumption of an extreme or prolonged contact between the two continents in Tertiary times on account of the large number of endemic families on either side of the Atlantic.

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